PRIMATE BEHAVIORAL RESPONSES TO BURNING AS A MODEL FOR HOMININ FIRE USE

by

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ABSTRACT

Both anecdotes and systematic observations show that primates take advantage of burned landscapes. However, few studies have made these behaviors the focus of attention. This dissertation includes three papers documenting the behavioral responses of South African vervet monkeys (*Chlorocebus aethiops*) to seasonal burning. The first paper details changes in spatial behavior related to burning. In it, we review the behavioral responses of other primate populations to fire, and describe typical ranging behavior among vervets. We compare our results to other accounts of primate-fire related behavior and evaluate whether the changes observed are unique to this population or species, or whether they are indicative of a primate-wide phenomenon. The second paper outlines changes in foraging opportunities postburn. Here, I compare the postencounter energetic returns and encounter rates of primate prey items within burned and unburned conditions. I identify improvements where they exist, and explore the hypothesis that burned savanna habitats offer improved foraging returns. Finally, the third chapter explores how and why fire alters both the threat of predation and general risk. I review the general pattern of predation on primates, and investigate the tradeoffs involved in risk avoidance. I conclude that burning offers savanna-dwelling primates a safe-haven from many primary predators and threats.

I end the dissertation with a fourth paper that employs conceptual tools from optimal foraging theory to generate, test, and refine expectations about the behavioral adaptations of hominins inhabiting fire-prone savanna biomes. Here, I use the primate data to construct a general theory of behavior for the origins of human fire use. I argue that the behavior of savanna-dwelling primates may serve as a basis for hypotheses

regarding the origins of fire use in the hominin lineage. I highlight the distinction between passive and active fire use, and use these observations to suggest future realms of research investigating fire-related behavioral shifts and their effect on the human life history, hominin dispersals, and the adaptation of complex pyrotechnology.

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CHAPTER 1

FIRE, TRAVEL, AND HOME RANGE EXPANSION: A BEHAVIORAL RESPONSE TO BURNING AMONG SAVANNA DWELLING VERVET MONKEYS (*CHLOROCEBUS AETHIOPS*)

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Fire and Home Range Expansion: A Behavioral Response to Burning Among Savanna Dwelling Vervet Monkeys (*Chlorocebus aethiops*)

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ABSTRACT The behavioral adaptations of primates to fire-modified landscapes are of considerable interest to anthropologists because fire is fundamental to life in the African savanna—the setting in which genus *Homo* evolved. Here we report the behavioral responses of a savanna-dwelling primate, vervet monkeys (*Chlorocebus aethiops*), to fire-induced ecological change. Using behavioral and spatial data to characterize ranging patterns prior to and postburn and between burn and nonburn years, we show that these primates inhabiting small, spatially bound, riverine habitats take advantage of newly burned savanna landscapes. When subjects encountered controlled fires, they did not flee but instead avoided the path of the fire seemingly unbothered by its approach. After fire, the primates' home range expanded into newly burned but previously unused areas. These results contribute to understanding the response of non-human primates to fire-modified landscapes and can shed light on the nature and scope of opportunities and constraints posed by the emergence of fire-affected landscapes in the past. Results also expose deficiencies in our knowledge of fire-related behavioral responses in the primate lineage and highlight the need for further investigation of these responses as they relate to foraging opportunities, migration, resource use, and especially fire-centric adaptations in our own genus. Am J Phys Anthropol 154:554–560, 2014.

Natural fires are a common feature of the dry season in many temperate biomes (Van Wilgen et al., 2004; Seydack et al., 2007), and man-made fire is a ubiquitous occurrence in tropical and subtropical Africa (Bird and Cali, 1998; Mapaure et al., 2009) where humans and other primate species often coexist. However, to date, no systematic investigation has focused on primate behavioral responses to fire (see Table 1 for a review of published and unpublished accounts). Relatively little is known about how primates are impacted by the large-scale habitat modification that often accompanies burning, nor do we know much about the immediate responses of primates to fire. Do primates follow the general mammalian pattern, instinctively fleeing when fires draw near (Lyon et al., 1978), or are they able to gauge the relative threat of fire and avoid it accordingly? Research among savanna-dwelling chimpanzees suggests the later. In a first-hand account of the immediate response of chimpanzees to seasonal burning, Pruetz and LaDuke (2010) illustrate these primates' savvy fire sense. Rather than flee from oncoming flames, subjects, who are accustomed to burning, calmly monitor fires showing little perceptible concern as flames draw near.

Where data regarding primates' behaviors postburning are available, researchers often note changes in prey choice and shifts in locomotion and ranging patterns. For example, in the aftermath of a bushfire, members of a reintroduced group of chimpanzees in Senegal were observed eating cooked *Afzelia* seeds (Brewer 1978). As Gouzoules recounts "rhesus macaques on the Island of Cayo Santiago have been observed searching for coconuts in the hot ashes of nearly expired fires, reaching in and testing to see if they had cooled enough to eat" (Armelagos, 2010:159). In addition to consuming cooked foods found in recently burned landscapes, primates also use burned corridors for travel. After fires, chimpanzees and vervets preferentially travel terrestrially in burned terrain rather than traveling through unburned vegetation (J. Pruetz, personal communication; Jaffe and Isbell, 2009). Researchers attribute this burn-zone preference to greater visibility and reduced travel costs—unburned subcanopy growth is often dense and difficult to move through. In addition to reduced travel costs, Jaffe and Isbell (2009) suggest a decrease in predation risk as motivation for burn-area travel. They hypothesize that, deprived of potential concealment, predators are observable at greater distances enabling terrestrially moving primates to engage in fewer and shorter vigilance events. Perhaps motivated by these changes to travel, Jaffe and Isbell's vervet subjects ranged further

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TABLE 1. Published and anecdotal post hoc primate–fire interactions

Species	Type of interaction	Reference
Cercopithecus aethiops	Travel through burn	Jaffe and Isbell (2009)
	Foraging in burn	Jaffe and Isbell (2009)
Cercopithecus sabaeus	Consumption of cooked seeds	Harrison (1983a, 1984)
Macaca fascicularis	Foraging in burn	Berenstain (1986)
	Consumption of cooked fruit	Berenstain (1986)
Macaca mulatta	Consumption of cooked fruit	Armelagos (2010)
Pan troglodytes verus	Fire tolerance	Pruetz and LaDuke (2010)
	Consumption of cooked fruit	Brewer (1978)
	Consumption of cooked fruit	S. Bogart, personal communication
	Travel through burn	J. Pruetz, personal communication
Papio Anubis	Foraging in burn	K. Hunt, personal communication
Papio cynocephalus	Range expansion in burn	Rasmussen (1983)
Papio ursinus	Foraging in burn	J. Beehner, personal communication
	Foraging in burn	L. Swedell, personal communication
Symphalangus syndactylus	Range constriction postburn, habitat deterioration	O'Brien et al. (2003)

Fig. 1. Representative photos of three primary plant communities within the study area prior to burning. Closed canopy *Olea europea subsp. africana-Rhus leptodictya* woodland (**A**), dispersed trees/savanna *Acacia nilotica-Acacia caffra* woodland (**B**), and dispersed trees/savanna *Lippia javanica-Loudetia simplex* shrubland (**C**). [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

from the refuge of riverine habitat than previously observed.

The above observations highlight the opportunistic behavior of primates around fire and suggest a pattern of tolerance, interest, and even exploitation of burned landscapes. Here we study the behavioral responses of savanna-dwelling vervet monkeys (*Chlorocebus aethiops*) to burning. We predict the monkeys will take advantage of landscape fires by altering their spatial patterns to incorporate newly burned areas. To explore this hypothesis, we compare ranging behavior before and after a prescribed burn as well as between burn and nonburn years. Our results help characterize primate-wide adaptations to fire-modified landscapes that should guide hypotheses about the use and control of fire by our own ancestors. These data are especially important since little is known about the sequence through which extreme fire dependence evolved in our lineage—despite the fact that controlled fire-use is "a unique and universal human practice" (Carmody et al., 2011, p. 1).

METHODS

Site location, fire, and subjects

We observed one troop of habituated vervet monkeys throughout the 2012 burning regime (February–July) at the Loskop Dam Nature Reserve (LDNR), Mpumalanga Province, South Africa. The LDNR is located within the summer rainfall region of South Africa's savanna biome (Mucina and Rutherford, 2006). Three separate weather stations have continuously logged climatological data for the Reserve over the past decade. Rainfall ranges from 400 to 900 mm per annum, with most precipitation occurring during the hot, summer/wet season (November–April). The transition to the cold, winter/dry season (May–October) is marked by decreased rainfall, lower mean temperatures, and shorter day length.

Three primary vegetation communities exist within the study area (Barrett, 2009): *Olea europea subsp. africana-Rhus leptodictya* woodland (*Olea*), *Lippia javanica-Loudetia simplex* shrubland (*Lippia*), and *Acacia nilotica-Acacia caffra* woodland (*Acacia*) (Fig. 1). The *Olea* vegetation community grows within and along riverine corridors and is characterized by tall (~20 m) closed canopy vegetation, a thick bushy understory, and sparse ground-level plants. The bordering *Lippia* and *Acacia* vegetation contain little or no closed canopy. In these habitats, tall grasses and small shrubs create significant ground cover and limit ground-level visibility. Larger trees are widely spaced and occur in small clumps or singly.

As part of a broad management plan, controlled burns are carried out annually within the Reserve. LDNR's fire ecologist selects burn sites based on the nature and location of natural fires, the need to create firebreaks, to

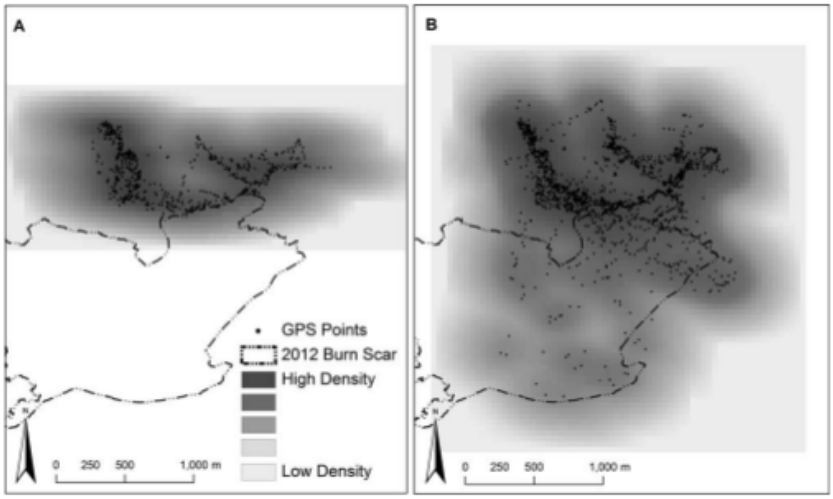

Fig. 2. Preburn (**A**) and postburn (**B**) KDEs of range use for the 2012 study year. Color gradation represents changing density distributions. Circles represent GPS points.

remove unwanted vegetation, to stimulate movement of game species, and to control parasites. Controlled fires are ignited several weeks prior to the onset of dry, winter weather. The timing of these burning events is critical as burning just ahead of the last rains of the season reduces the risk of runaway fires and promotes quick regrowth. In collaboration with park staff, the 2012 controlled burns were ignited near the study area. These fires burned large areas of *Lippia* shrubland and *Acacia* woodland habitat south and southwest of our subjects' home range. However, only a small portion of the observed pre-burn home range was impacted by burning (see Figs. 2 and 3).

The habituated troop of vervet monkeys that were the focus of this research have been semicontinuously studied since 2006. Throughout this time, their range and composition have remained relatively stable. At the onset of the 2012 project, the troop consisted of 10 adults (four male, and six female) and 13 immatures. One adult male from an adjacent troop successfully joined the study troop during the last 2 weeks of 2012 data collection. A second adult male attempted to join the study troop earlier in the season but was only intermittently present. To document the vervets' responses to fire and modifications in behavior following the burn, we began monitoring their ranging patterns 3 months prior to the anticipated controlled burning event and continued collecting observational and spatial data for 3 months following the burn.

Behavioral data collection

We implemented both instantaneous scan sampling and focal follows (Altmann, 1974). Instantaneous scans were conducted every 15 minutes with an observational window of 5 minutes. During scans, researchers collected the following data for each observable individual: habitat and subhabitat, successional re-growth stage (for postburn observations), age, sex, and behavior. Researchers conducted 20 minute focal follows once every hour. Focal follows were limited to adult, subadult, and juvenile subjects. Infants were excluded. During follows, the behavior of a single vervet was documented. For each follow, observers recorded the duration of time spent in any given habitat and subhabitat, along with the duration and nature of all behavioral sequences within each habitat. These data were collected with Cyber Tracker (www.cybertracker.org) software on Trimble Global Positioning System (GPS) units. To capture unique behaviors in the presence of fire and in fire-modified landscapes, we also conducted ad libitum follows. Where behavioral data are used to compare habitat-use after burning, we compare proportions of time in any particular habitat by dividing the amount of time spent in each habitat by the duration of the focal follow for each focal subject.

Spatial data collection

At the onset of each troop scan (15-minute intervals) we collected GPS points, first moving as close as possible to the center of the troop. As such, GPS data points reflect troop movements rather than individual movements. We used a Trimble Juno ST GPS unit to record spatial data and transferred all spatial data via Terrasync software to ArcGIS 10.1 for analysis. We compared the study troop's burn-year spatial patterns to those of a nonburn year. Non-burn year data were collected in 2007 by A. Barrett (2009). Barrett's spatial data collection methods were similar to ours. However, the frequency of point collection differed; Barrett took GPS points at 1-minute intervals while the troop was moving and at 30-minute intervals while the troop was stationary. To compare the 2007 dataset to that of 2012, we examined only data collected during the same months (February–July) and used only GPS points taken at intervals greater or equal to 15 minutes.

Spatial analyses

To systematically study changes in ranging behavior as they related to fire, we compared ranging behavior preburn to ranging behavior postburn during the study

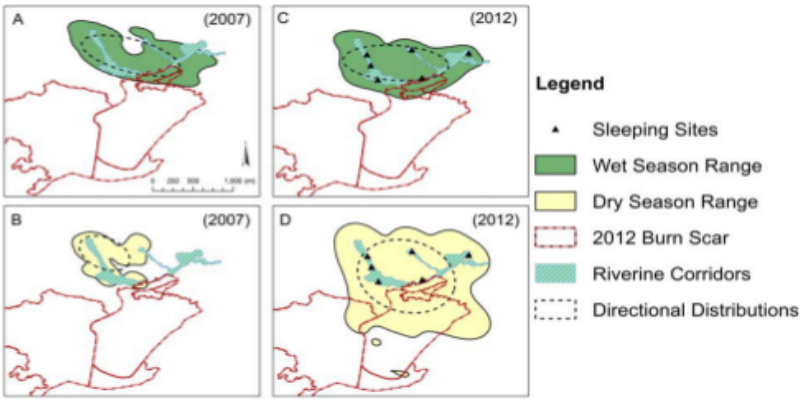

Fig. 3. Wet (**A**) and dry (**B**) season home ranges during a nonburn year (2007). Wet (**C**) and dry (**D**) season home ranges during a burn year (2012). Directional distribution ellipses show the direction of dispersal and central tendencies of movement during each of the seasons. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

year (2012). We split these spatial data into GPS points collected preburn ($n = 720$ GPS points) and postburn ($n = 1{,}949$ GPS points). We then used Geospatial Modeling Environment software (Beyer, 2012) to generate Kernel Density Estimates (KDE) (kernel = Gaussian, bandwidth = LSCV [least squares cross validation algorithm], cell size = 40 m) for preburn and postburn ranges (Fig. 2). KDEs are nonparametric estimates of a variable's probability density function where a finite set of data is used to predict population level spatial trends. KDEs are compared to examine changes in the distribution and frequency of spatial use.

To assess whether the spatiobehavioral patterns observed during the burn year were related to seasonality rather than burning, we compared the 2012 data to the nonburn year's data. We used long-term climatological data for LDNR that showed the seasonal transition from summer/wet to winter/dry weather occurred in late April/early May. On the basis of that record, we split both the 2012 and 2007 spatial data into two seasons: wet (January to April [2007 GPS points $n = 1{,}138$; 2012 GPS points $n = 1{,}277$]) and dry (May to July [2007 GPS points $n = 941$; 2012 GPS points $n = 1{,}282$]). We then calculated KDEs, by season. For comparison, we transformed the KDE output vectors into surface maps and added isopleths (bounding elements) around each KDE surface at a 95% inclusion factor. The resulting shapes represent wet and dry season home ranges for each year (Fig. 3).

In addition, we conducted directional distribution analyses for the wet and dry season of each year using arcGIS 10.1 (Fig. 3). Directional distribution analyses measure the direction of dispersal and central tendencies of movement within any spatial dataset. The result of the directional distribution analysis is an ellipse polygon which covers all data points within one standard deviation from the spatial mean (approximately 68% of all spatial features are encompassed by each ellipse).

RESULTS

Vervet responses to burning

Results from ad libitum follows on the dates of controlled burns suggest that subjects were able to assess the risk of approaching fires. Unlike other animals that flee from fire, the vervets did not show any signs of fear or stress as the flames neared. While most members of the troop appeared relatively uninterested in the blaze, at least one individual monitored its approach. The following are accounts of behaviors observed.

On April 2nd at 12:00 hours, the observer (CP) first noted the presence of smoke approximately 200 m southwest of the ravine where the troop was collectively feeding along the margin of *Olea* woodland habitat. At that time, there was no reaction to the smoke from subjects. By 13:00 hours the fire had become audible, and the smell of burning vegetation was strong. One juvenile and one adult female climbed into a tall tree to scan toward the smoke. At 13:30, the flames became visible and appeared to be moving toward the troop. Despite the nearing blaze, troop members continued foraging, and in so doing moved further into the *Olea* woodland canopy, and out of the path of the approaching fire. By 14:30 the troop had moved far enough from the fire that the smell and noise were no longer perceptible.

On April 3rd, an observer (NH) noticed the blaze at 11:15 hours as it crested a hill and began to move downslope toward foraging troop members. Flames were visible at a distance of approximately 100 m. At this time, one adult male scanned toward the fire while the remaining subjects continued to feed in a densely treed *Olea* woodland riparian corridor. At 11:30, the focal male moved toward the fire and climbed the tallest nearby tree to observe. He was followed by one subadult male. At 11:45 the focal adult male descended from his post and moved closer to the flames to feed in a large *Olea europea* tree at the edge of the *Olea* woodland habitat. The subadult male rejoined the troop members foraging nearby. The focal adult male fed for only 3 minutes after which, he climbed into a smaller tree within the *Acacia* woodland habitat closer to the flames. By 12:00 hours the fire was within 50 m of the subject. At 12:05 the focal subject moved higher in the tree and scanned in all directions. The flames were less than 20 m from the focal by 12:08, at which time he descended from the tree and joined the troop, which had traveled approximately 100 m away from the blaze. All troop members continued to forage in an *Olea* wooded drainage, moving away

from fire. At no time did any member of the troop appear panicked by the nearby flames. By 12:30, the fire had terminated at a natural fire break and troop members had moved approximately 200 m away. At 13:15, the troop reversed its direction of travel and returned to the location of the burn. Their path skirted the perimeter of the burn, but no individuals were observed within the newly burned patch.

Habitat use and home range

Prior to burning, subjects' ranging patterns were consistently tied to three primary drainages where they spent the majority of their time. Postburn, individuals spent a significantly larger proportion of their time outside of the *Olea* vegetation of riparian corridors. When we compared the average proportion of observed time in *Olea* woodland habitat across all 2012 focal follows for each subject, the mean percentage of time each subject spent in the *Olea* woodland habitat preburn ($n = 17$ subjects, $\overline{M} = 0.63 \pm 0.18$ [SD]) was greater than the percentage of time spent in *Olea* woodland habitat postburn ($n = 20$ subjects, $\overline{M} = 0.41 \pm 0.16$ [SD]). The difference was significant when measured with a Student's paired t-test ($t = 3.76$, df = 14, $P = 0.002$). Not only did the subjects explore these new areas, but they used them frequently enough that they became incorporated into the postburn range (Fig. 2)—resulting in a measurable expansion in range size (preburn range = 1.03 km^2, postburn range = 1.97 km^2). Expansion primarily occurred in burned areas rather than appearing as general diffusion at all territorial boundaries. While no new sleeping sites were established within the burned area, subjects shifted from exclusive use of sleeping sites on the northern boundary of the preburn range, to sites along the southern portion of the preburn range (see Fig. 3). Southern sleeping sites were much closer to the newly burned territory and facilitated faster access to it. To quantify patterns in sleep site selection, we scored each day's sleep site based on its location (north = 1, south = 0, and intermediate = 0.5). We compared the scores for preburn dates ($n = 26$) to those from after the fire ($n = 57$). The mean preburn score was 0.81 ± 0.37 (SD), and the mean postburn score was 0.54 ± 0.48 (SD). The preburn and postburn patterns were significantly different (Welch's two sample t-test, $t = 2.70$, df = 61.43, $P = 0.008$), with utilization of southern sleep sites a common postburn occurrence.

To investigate whether the observed expansion was related to dry season shifts in foraging range rather than fire induced change, we split the spatial data from burn and nonburn years by season and compared the spatial patterns. When KDEs from each year and season were compared, the 2012 pattern appears even more pronounced (Fig. 3). In 2007, the total range size from wet season to dry season decreased by 46% (wet season range = 0.90 km^2, dry season range = 0.48 km^2). In contrast, home range size increased by 122% between the 2012 wet and dry seasons (wet season range = 1.09 km^2, dry season range = 2.43 km^2). Riverine habitats remained core areas during the 2007 dry season and forays into more open savannah-like settings decreased. In comparison, the 2012 dry season expansion was broadly diffused and the study troop spent a majority of time far outside of riverine habitats rather than within them.

While vervet home ranges are typically centered on riparian, or canopied habitats, forays outside of these areas can be driven by access to water. Both Wrangham (1981) and Harrison (1983a) document subjects traveling outside of established home ranges to access water during periods of drought. We also observed vervets drinking at a distant water source postburning, and access to this reservoir was only possible via travel through burned corridors. To explore the likelihood that decreased water availability drew our subjects into the burned area, we compared climatological conditions between the study and control years. If average daily temperatures were higher, and daily precipitation lower during the study year, then perhaps our subjects experienced a local water shortage which forced them to travel further to acquire this resource. However, climatological patterns during the study and comparison years were not significantly different (Student's paired t-test, $n = 182$ dates [February–July 2007 and 2012]; rainfall, $t = -1.157$, df = 153, P value = 0.249; average daily temperature, $t = -0.026$, df = 149, P value = 0.979), suggesting that subjects faced similar constraints during both years. Additionally, subjects' use of water sources in unburned habitats did not appear to change postburning. The percentage of each subject's focal follows that recorded drinking bouts at the reservoir were not statistically different from the percentage of their postburn follows that recorded drinking bouts at water sources located in unburned habitats (Student's paired t-test, $n = 20$ subjects, $\overline{M}$ unburned water source = 0.038 ± 0.02, $\overline{M}$ reservoir = 0.013 ± 0.02, $t = 0.372$, df = 18, $P = 0.714$). These results suggest that water acquisition at the reservoir was merely supplemental to drinking bouts at continuously available water sources in unburned habitats.

DISCUSSION

Fire and expanding home ranges

Of the savanna-woodland dwelling primates, vervets inhabit the smallest and most ecologically bound territories (Struhsaker, 1967; Cheney, 1981; Isbell et al., 1990). Generally, troops establish territories along primary drainages, which are bordered by adjacent groups. Extended excursions into surrounding savanna habitat are rare (Isbell et al., 2002), and shifts in core home ranges, when they do occur, are often associated with increases in group size (Isbell, 1991) or habitat deterioration (Isbell et al., 1990). But, because vervets commonly defend home range margins from neighboring troops (Struhsaker, 1967; Wrangham, 1980; Harrison, 1983b; Isbell et al., 1990), options for expansion and dispersal are limited. Additionally, rates of mortality are higher in unfamiliar areas, especially if those areas are comprised of habitat with fewer trees (Isbell et al., 1990).

The range expansion documented in this study deviates both from the common vervet pattern and from the seasonal ranging pattern of the same troop during previous years of study. Rather than displacing or fusing with neighboring troops along riverine corridors, our subjects moved into uninhabited savanna. Average rainfall and daytime temperatures during the study year were not statistically different from previous years, and water sources within unburned areas were consistently available throughout the observational period suggesting that climatological change did not drive the range shift. While troop size did increase, the addition of one member months after the burn is not likely to have caused the large scale expansion we documented. In the absence of these causal factors, we suggest that the 2012 pattern was driven by fire-mediated habitat modification. We

hypothesize that our subjects' preference for new, savanna territory was related to positive changes in foraging efficiency within the burn.

Positive changes in foraging efficiency can be related to either search improvements or decreased handling costs. Burning can affect both. For example, low intensity grass fires quickly and effectively eliminate vegetative understory, improving search conditions by exposing otherwise concealed food sources such as fallen nuts and seeds, animal burrows (Fisher, 1948; Bird et al., 2005), and tubers (P. Wiessner, personal communication). Post-encounter, fire can decrease handling costs in two ways: 1) eliminating or reducing pursuit effort and 2) increasing prey bionutrient availability via cooking.

Humans have traditionally used fire and/or smoke as a tool to pacify, disorient, and immobilize insect and animal prey (Fisher, 1948; Christensen, 1980; Mistry et al., 2005). However, even natural fires may render pursuit times for mobile prey such as animals and insects null if those prey become stunned or killed during the blaze. Innovative foragers able to predict the speed and direction of fires could easily collect immobile prey items after the fire has passed. Second, cooking denatures proteins, lowers pathogen loads, and softens dry or brittle tissues all of which allow for more effective digestion and better absorption of the nutrients within cooked foods (Oka et al., 2003; Dominy et al., 2008; Carmody and Wrangham, 2009). Prey items cooked by the fire should therefore be an appealing resource and again should be subject to reduced search costs.

In addition to immediate foraging improvements post-fire, delayed foraging opportunities in burned habitats may also exist. For example, the new shoots that emerge postburn are an appealing food source to many savanna dwelling species, especially as other plant foods become desiccated or unavailable during the dry season (Archibald and Bond, 2003; Sensenig et al., 2010). Alternately, new forage may create stable prey aggregates by drawing invertebrates into burned patches to feed (Berenstain, 1986). Ultimately, each of these mechanisms can alter the foraging choices of a consumer, potentially pulling spatially tethered species into new habitat—as reported here. However, without detailed dietary analyses, hypotheses regarding positive postburn foraging opportunities for our vervet subjects remain speculative.

Primates and fire, the phylogenetic legacy

Results presented here suggest that fire provided an opportunity for vervets to take advantage of territory that was otherwise unexploited. By moving through burned corridors, subjects ranged farther than ever previously observed. Not only did they explore new territory, they stayed there. The positive response of our subjects to burning, and their change in ranging patterns to take advantage of the burned area, was remarkable. We expect that larger brained hominin ancestors inhabiting Plio-Pleistocene Africa would have been capable of at least as much behavioral flexibility, thus posing an important challenge to scenarios attributing the origins of fire use in our lineage to a lucky accident.

Our results contribute to a more fine-grained account of the ways in which non-human primates use fire-modified landscapes and begin to shed light on the nature and scope of both the opportunities and constraints posed by the emergence of fire-affected landscapes in the past. While the importance of fire in human evolutionary history has long been acknowledged (Clark and Harris, 1985; Goudsblom, 1986; James et al., 1989; Pyne, 1995; Wrangham et al., 1999; Burton, 2009; Wrangham, 2009), how and why early hominins came to use this force is largely unknown. Descriptions of primates' exploitation of burned landscapes provide strong evidence that they understand fire and attendant changes to travel and foraging opportunities. That even the most terrestrially constrained of savanna-dwelling primates expand into burned territory suggests a deep phylogenetic history of fire tolerance and pyrophilic tendencies. Pruetz and LaDuke (2010) argue that savanna chimpanzees' ability to "conceptualize" fire is a synapomorphic trait within the human–chimpanzee clade. We agree, but given that our vervet subjects exhibited a similarly "conceptualized" response to fire—they did not flee but instead calmly monitored the approaching blaze as the flames, noise, and smoke drew near—argue for an even deeper history of the trait within the primate clade. The fire-positive adaptations detailed in this and other savanna-dwelling primate populations provide clues to understanding the foundation for complex pyrotechnological innovations in our own lineage. If burned landscapes represent novel foraging opportunities, consistent and controlled use of these patches would have contributed to the selective pressures that shaped the unique morphology, mobility, and behavior of our genus.

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CHAPTER 2

WHAT'S BURNING GOT TO DO WITH IT? PRIMATE FORAGING OPPORTUNITIES IN FIRE-MODIFIED LANDSCAPES

2.1 Abstract

Anecdotal and formal evidence indicate that primates take advantage of burned landscapes. However, little work has been done to quantify the costs and benefits of this behavior. Using systematic behavioral observations on a population of South African vervet monkeys *(Chlorocebus aethiops*), I evaluate changes in their foraging opportunities following a series of controlled burns. Postburning, vervet subjects traveled far outside their normal range into burned savanna. Why were they drawn to this otherwise distant landscape? I test two hypotheses. First, that burning improves encounter rates with high ranking prey. Second, that fire reduces postencounter handling costs, raising profitabilities for certain foods. Results show that burning significantly improves encounter rates for two important prey types, invertebrates and leaves. Fire does not appear to significantly improve the postencounter profitability of any resources. Results highlight the foraging benefits that likely contributed to the range expansion and exploitation of burned savanna habitats previously documented. These quantified benefits have broader implications for the evolution of fire-use in our own lineage.

2.2 Introduction

Like other animals inhabiting fire-prone environments, savanna-dwelling primates take advantage of newly burned landscapes. Two recent reports detail differences in

primate ranging behavior following a fire (Chapter 1; Jaffe and Isbell 2009; Herzog et al. 2014). In each, vervet monkeys foraged in burned habitat not previously exploited, and range size grew substantially to include burned areas. Other published and anecdotal reports suggest possible draws for primates in burns include fluctuations in insect prey and recently cooked foods (for a review see: Chapter 1; Herzog et al. 2014). However, relatively few studies synthesize the behavioral responses of animals regularly exposed to burning (but see: Green et al. 2014), and until now, none have made primate behavior around fire the primary target of investigation. As a result, no comprehensive picture has yet developed of the broad range of interactions that other members of our own order have with landscape fires (Parr and Chown 2003; De Ronde et al. 2004). These data are important not only for understanding the observed behaviors, but also because the effects of burning on foraging payoffs can contribute to the debate surrounding the evolution of obligate fire-use in our own lineage (Burton 2009; Wrangham 2009; Parker 2014; Parker et al. 2015).

To assess the potential foraging improvements fire may provide to savanna-dwelling primates, I rely on the theoretical and mathematical framework of Optimal Foraging Theory (Stephens and Krebs 1986) to construct hypotheses regarding burn-use. Predictions generated from optimal foraging models help researchers explain foraging variability within and across taxa (Pyke et al. 1977; Stephens 2008; Davies et al. 2012), and the link between diet breadth and time allocated to either search or handling has important implications for understanding changes in subsistence-related behavior (Hawkes and O' Connell 1992). Despite the frequent use of optimal foraging theory as an heuristic tool in human studies (for a review of archaeological applications see: Bird and O'Connell 2006; Codding and Bird 2015, for ethnographic applications: Kelly 2013), its use in primatological research is limited. As noted by Sayers et al (2010): "Although direct tests of OFT models are scarce… a number of primatologists have referenced foraging theory as an a posteriori tool to explain observed behavior" (for *a priori* applications see: Nakagawa 1989; Nakagawa 1990; Grether et al. 1992; Altmann 1998; Baritell et al. 2009;

Sayers et al. 2010).

Optimal foraging models focus on the economics of nutrient acquisition and the decisions foragers make about resource exploitation (Stephens and Krebs 1986; Stephens 2008). Foraging behavior is assumed to optimize nutrient returns given local ecological constraints with changes in foraging behavior consequences of changing ecology. In the classic prey model (Charnov 1976a; Stephens and Krebs 1986) an individual forager's goal is to maximize net rate of energy intake. The model poses the foraging decision as a single, repetitive, yes/no choice that depends on the profitability, the rate expected for handling a food item just encountered, compared to the rate expected for continuing to search for something better. The currency in which the alternatives are measured is typically rate of energy acquisition (kcal/hr). Resources are ranked by their expected net profit of energy per unit of time spent in handling (postencounter return rate). Highest-ranked resources are always included in the optimal diet with lower-ranked resources added or dropped in order of profitability depending on encounter rates with higher ranked resources. The model assumes that resources are encountered randomly relative to their abundance within the patch. The model partitions total foraging time into two mutually exclusive activities, searching and handling. Alternatively, the Patch Choice Model (MacArthur and Pianka 1966; Charnov 1976b), identifies the tradeoff between earned returns within a patch and travel time between patches in an environment where resources are clumped instead of randomly distributed. In the Patch Choice Model, a forager's goal is to maximize the net rate of return per unit foraging time by exploiting the optimal array of patches. Decision variables in the model are: enter a patch or bypass it to travel to (search for) another with a higher rate. The Patch Model treats patches as the Optimal Diet Model treats individual prey items.

Here, I use these models to investigate changes in encounters and foraging return rates for a population of savanna-dwelling vervet monkeys (*Chlorocebus aethiops*) following a fire. I expect that vervet food items will be unevenly distributed across the landscape and therefore take advantage of both patch choice and prey choice

simplifications. In this study, I follow others (Schoener 1974; Stephens and Krebs 1986; Schoener 1987; Sayers et al. 2010) in operationally defining all food resources as individual prey whether they occur as aggregations/patches, like berries from a bush, or as singular items. I define an encounter as a subject first initiating contact with a prey item. Postencounter, I use the inclusive term "handling event" to describe the combined amount of time spent in pursuit and consumption. Here, pursuit, whether failed or successful, involves active engagement with a particular resource (for mobile resources this includes chasing, for sessile resources such as tubers this may include digging). I calculate the rate of energy gained by a forager for each handling event based on the total energy of the prey item/s consumed and the amount of time spent in handling (expressed in these analyses as kcal/min, see below).

I test two hypotheses about the net foraging benefits underpinning documented range expansions. My first hypothesis is that, burning reduces search costs by increasing encounter rates for food resources that remain postburn. Observations among contemporary hunter-gatherers exemplify fire as a tool to increase encounter rates with profitable prey (Bird et al. 2005; Bliege Bird et al. 2008; Codding et al. 2014). Fire can improve encounters with sessile resources by decreasing groundcover and increasing visibility, exposing resources otherwise concealed by plant growth (Gowlett 2010). For mobile prey, fire may improve encounters both by improving visibility and by altering the prey's spatial patterns. These improvements may occur in two temporally distinct phases. Immediately postfire vertebrate and invertebrate prey may flee to unburned or sheltered refugia within the broader landscape of the burn. Aggregated here, they may be easy targets for foragers. For example, Jaffe and Isbell (2009) suspect that vervets at Segara Ranch were attracted to exposed populations of *Crematogaster* spp. which had evacuated acacia thorn domatia for the safety of deeper crevices at the bases of host-trees during a fire. As the invertebrates emerged from tree bases to repopulate their domatia, they became susceptible to predation. A second influx of mobile prey may come several weeks after a fire, when invertebrates return to burned areas to feed on abundant seed-fall and

nitrogen-rich new shoots (Andersen 1988; Swengel 2001).

Second, fire will significantly increase postencounter return rates (i.e., the profitability) of certain resources. Profitiabilities are shifted when the amount of time dedicated to handling a resource is altered. Fire may reduce handling times for prey items in several ways. First, fire may stun, immobilize or otherwise alter the behavior of mobile prey making them easier to capture postencounter. Changes to postencounter pursuit are largely expected to occur among invertebrate prey. Second, fire/cooking may alter the mechanical and physiological properties of some plant and animal foods making them easier to process. Mechanical and physiological changes are expected to occur across all prey types, but will be especially apparent in two resource categories: seeds/nuts and underground storage organs (USOs). For seeds and legumes, cooking or parching can reduce the amount of work spent on extricating seeds from woody chaff by either prompting the release of seeds (seedfall) or by charring already exposed organs. For USOs, fire can gelatinize starchy tissues and reduce the work of fracture (Wandsnider 1997; Dominy et al. 2008; Zink et al. 2014). Therefore, when found, cooked or charred USOs and seeds may be consumed at a faster rate.

The results of this study are consistent with the first hypothesis; some prey were encountered significantly more often in burned areas. However, significant changes in postencounter profitabilities were not detected. As such, the results suggest that improved encounters alone can motivate changes in foraging behavior. Because primates in this study were able to both calmly avoid the path of the fire (Chapter 1; Herzog et al. 2014), and capitalize on the foraging opportunities fire created, we take a position similar to Pruetz and LaDuke (2010) in asserting a deep phylogenetic foundation for passive fire exploitation in the primate clade. Results prompt continuing investigation of foraging benefits for primates in burned landscapes because they provide an analog for those benefits available to early hominins from which obligate fire use evolved in our genus (Burton 2009; Wrangham 2009; Parker 2014; Parker et al. 2015).

2.3 Methods

2.3.1 Study site and subjects

The foraging behavior of one troop of habituated vervet monkeys (*Chlorocebus aethiops*) was studied during the 2012 burning regime (February–July) at the Loskop Dam Nature Reserve (LDNR), Mpumalanga Province, South Africa. Over the course of the study troop size ranged from 23-25 individuals (four-six adult males, seven adult females, five subadults, four juveniles, and three infants). Study subjects' home range (Figure 2.1) is comprised of three primary vegetation communities (from Barrett 2009): *Olea europea* subsp. *africana-Rhus leptodictya* woodland (*Olea*), *Lippia javanica-Loudetia simplex* shrubland (*Lippia*), and *Acacia nilotica-Acacia caffra* woodland (*Acacia*). *Olea* vegetation is primarily located within and along dongas (steep-edged drainages) and is characterized by tall (~20m) closed canopy vegetation, a thick bushy understory, and sparse ground-level plants. Bordering *Olea* habitat is a dense shrub-woodland, *Acacia*, which contains little or no closed canopy. In *Acacia* habitats, short grasses and small shrubs create significant ground cover and limit ground-level visibility. *Lippia* shrublands are situated at the edges of Acacia woodlands. These shrublands contain few large trees. Between trees, broad swaths of tall (up to 2 m) grass are common. Within tall grasses, visibility is extremely limited.

Burning at the study site occurs annually as part of a fire management plan (Eksteen 2003). Burn site selection is made by the park fire ecologist, and is carried out by fire maintenance staff. Burn sites are selected based on several criteria. First, management assesses the overall occurrence and location of natural fires. If the impact of natural fires has been limited, controlled burns will likely be implemented to suppress plant growth (annual grasses that have grown over a height of 1.5 meters, wooded areas that have not been burned within the past five seasons). Second, because the reserve aims to facilitate game viewing, grasses and herbaceous plants obscuring roadside views may be targeted for burning. Third, burns are carried out at the onset of the dry season to promote and stimulate the growth of new grass, especially as other forage becomes

desiccated. Finally, burning is used as a tool for reducing the presence/abundance of animal parasites including various species of tick (Barrett 2009; Filmalter 2010). To reduce the risk of runaway fires and to promote quick regrowth, burning typically occurs within the last few weeks of the wet season. In 2012, Park fire ecologists and staff ignited several small fires on April 3rd and 4th. These fires primarily impacted *Lippia* shrubland and *Acacia* woodland habitats located to the south and southwest of the subjects' preburn home range (for fire location see Figure 2.1). Approximately 343 hectares of land were burned. Of the plant communities in and surrounding the vervets' preburn home range, the plant community in which they spent most time, *Olea*, was only minimally affected; a bigger but relatively limited area of *Acacia* woodland was also impacted; and large swaths of *Lippia* shrubland south of the troop's preburn range were burned. Postburning, the vervets expanded their home range to include much of this newly burned, but previously uninhabited *Lippia* habitat (see: Herzog et al. 2014).

2.3.2 Behavioral data collection

To assess pre- and postburn foraging behaviors I conducted focal follows (Altmann 1974) throughout each observational day. Observers conducted focal follows once each hour for a duration of 20 minutes. Follows began in the AM at first troop encounter and ended in the evening after subjects had settled at a sleeping site. The first focal subject of the day was chosen randomly, following the first focal others were selected in an alternating male-female pattern without replacement (when possible). During each follow, the behavior of a single vervet was documented. Each observed behavior was timed, and the following data recorded: habitat, subhabitat, and burn status (for postburn observations). For tests of our predictions about changes in foraging return rates, researchers focused explicitly on feeding behaviors. I distinguish pursuit (individual has identified a food and is actively working to obtain or extract it) and consumption (individual has obtained a food and is consuming edible portions). Within the consumption category, edible items were classified by plant part (leaf, seed, pod, flower,

fruit, USO [may include a range of plant storage organs including: tubers, rhizomes, corms, and taproots], or animal category, vertebrate or invertebrate). Additionally, where consumption was observed, the number of bites per handling event was recorded. Behavioral sequences were digitally recorded using Trimble GPS units with Cyber Tracker software (www.cybertracker.org). Over the course of the study, 694 focal follows were recorded (totaling 232 hours of observation). However, in order to compare spatially but not temporally distinct foraging efforts in burned vs. unburned areas, I restrict analyses to postburn focal follows and include only data collected from adult and subadult subjects. These data include 469 focal follows, 111 of which document activity in burned habitats. Because no handling events were observed in burned *Olea*, the data I examine are limited to comparisons between burned and unburned *Acacia* and *Lippia* plant communities.

To generate a list of all foods encountered in each of the two habitats impacted by the fire (*Acacia* and *Lippia*), I combed through behavioral data and identified all prey items that were both available and in the diet (foods that were pursued or ingested during at least one handling event in both burned and unburned areas). Because some prey species were infrequently taken, I lumped resources into six categories (fruit [*Bridelia molis*, *Combretum zeyheri*, and *Grewia flavescens*]; gum; invertebrate; leaf [Clover spp, *Crassula* spp. various grasses, new shoots]; seed [*Acacia caffra*, *Acacia karoo*, *Acacia nilotica*, and *Acacia robusta*]; and USO). To address the issue of energetic variance within prey type categories containing more than one species, I compared the E_i (see E_i calculations in Tables 2.1 and 2.2) of each species within each type using a Tukey's Honest Differences test. No significant differences ($p < .05$) were detected for the fruit or leaf prey sets. For the seed prey set, one species, *Acacia nilotica* was significantly different from the others. However, the number of observations for this species is very small (n=6 handling events) so I include it here despite its variance. I calculated encounter rates for each prey type by summing the total duration (in seconds) of each focal follow, subtracting both time spent in nonforaging activities (resting, socializing, vigilance, etc.)

and time spent handling, then dividing the remaining time (time spent searching) by the number of discrete handling events observed for each prey type. Some follows included time in both burned and unburned habitat, where this occurred time was split according to the burn status of the habitat. Failure to pursue a prey item known to be available was quantified as a "zero encounter" because I cannot detect encounters without pursuit.

The rate of energy gained by a forager while pursuing any given prey is calculated based on the total digestible energy per item and the time spent in pursuit and handling (for mathematical equations see Table 2.2). I calculated profitabilities in several steps. First, to calculate the total digestible energy per item, I collected 23 commonly consumed items and measured the nutrient and nonnutrient content of each (Table 2.1). To obtain plant samples, I gathered ~200 grams of each plant part during monthly phenological surveys. After collection, wet samples of each were weighed whole. To obtain average weights, I measured approximately 50 individual seeds, fruits, or fruit pulps. Fruit pulp weight was determined by subtracting the seed weight from the fruit total weight. After wet weights for edible parts were obtained, I dried the samples at 40˚ C for 48-72 hours.

Once samples were dried I ground them and shipped 100 grams of each to the University of Free State Animal Nutrition Laboratory for organic matter, crude protein, fat, and neutral-detergent fiber (NDF) analyses. I used these results to estimate the metabolizable energy (ME) in each prey item following the methods outlined in Conklin-Brittain et al. (2006). I calculated ME using a low-fermentation assumption (ME1) (Table 2.2) because data suggest that vervets are able to effectively ferment some fiber (Conklin-Brittain et al. 1998; Isbell et al. 2013). In the low-fermentation formulation, sources of metabolizable energy include fat, protein, carbohydrates, and a small amount of fermented NDF. Because I was unable to conduct ash analyses on my plant samples, I used estimates from published data to supplement my own (Wehmeyer 1986; A. A. Aganga et al. 1997; Zamora et al. 2001; Nakagawa 2003; Isbell et al. 2013). Where direct measures were unavailable I used estimates from closely related species, and where no close analog was found I used conservatively low estimates (see notes to Table 2.1). When possible,

fruit seeds were removed and only pulp was sent for analysis. For some fruits I was unable to extract the pulp from the seed. In these cases (*Celtis africanus*, *Olea europea*, *Grewia flavescens*), entire fruits were sent for analysis. Because seeds of these species were either spat out or passed undigested by vervets, I offset the total ME of these species by 30% to discount for the energetic contribution of the seed. Due to insufficient sample sizes of invertebrates and gum, ME for these prey types were calculated using a composite of several species. For gum, composite species included: *Acacia karoo*, *Acacia tortilis*, and *Combretum zeyheri*. The invertebrate composite included: *Nephila senegalensis*, *Zonocerus elegans*, and *Crematogaster* spp. Field researchers were unable to collect any samples of USOs. Energetic data presented here are from a semi-arid adapted rhizome (*Romulea* sp.) similar to the suspected target species taken during this study (Bennett and Jarvis 1995).

Second, I calculated ingestion rates (IRs) for each prey type by summing the amount of time spent handling a resource and dividing by the number of bites of that resource taken (Table 2.2). I used IR averages to fill in missing data, where bite quantities for a given handling event were unknown. Handling events in which the prey type was unknown were eliminated from the data-set. For handling events where species-specific ME or IR were unavailable, the average ME or IR for that prey type (i.e., fruits, seeds, etc.) was used in calculations. For the purpose of these analyses, we assume that a handling bout ends after bites are no longer taken. Although prey items continue to be processed through both oral manipulation and digestion long after the last observable bite, integration of internal handling costs are beyond the scope of this study. Here, I rely only on the observable phenomena of bites taken and time spent delivering bites to mouth. For reviews of issues related to primate digestion see Lambert (1998) and Milton (1984); for cercopithecine specific digestive retention times see Blaine and Lambert (2012).

Finally, I combined these ingestion rate data to calculate the postencounter return rate, or profitability, for each handling event (E_i). To do this, I multiplied the metabolizable energy per prey species bite by the total number of bites taken during the handling event

(Table 2.2). Following first contact with prey, any time spent in pursuit, extraction, or consumption was considered part of the handling event. After I had calculated the profitability of each handling event, I split the handling events into categories based on the burn status of the habitat in which they occurred.

2.3.4 Statistical analyses

Like many ecological and abundance variables, our encounter counts include a large number of zeros. Observed zero counts may be driven by two different processes: 1) foods were not detected/available, or 2) available foods were detected by the forager but were not pursued. Because observers were unable to distinguish between these two classes of zeros, they treated both as a "zero encounter" regardless of the underlying rationale. Simple linear regression models, such as Poisson, are insufficient for handling this type of data because they are unable accurately estimate overdispersed data. To determine the effect of burning on encounters I compared two model classes, each designed to manage zero-inflated or overdispersed data. The first model class, zero-inflated negative binomials (ZINB), are tailored to deal with a high frequency of zero counts by implementing two linear models to estimate the probability of obtaining a zero value: a logit model accounts for the binary encounter-no encounter interaction, and a Poisson model measures the magnitude of the interaction once an encounter has taken place (Zuur et al. 2009; Cameron and Trivedi 2013). ZINB models were constructed for each prey type, and fitted using the zeroinfl function of the pscl statistical package in R (R Core Team 2012). I also constructed Negative Binomial Generalized Linear models (GLMNB) for each prey type. GLMNB models were fitted using the glm.nb function within the MASS package. I compared the outcomes of the two model classes using Vuong's nonnested test. The negative binomial models provided the best fit, and I report only their results below.

To determine if burning had an influence on postencounter returns (E_i), I constructed linear mixed-effects models using the lmer function of the lme4 package in

R. Models included burn status (coded as 0 for unburned and 1 for burned), prey species, date, and habitat as fixed effects, and focal ID as a random effect. I compared all possible models built with these predictor variables using Schwarz's Bayesian information criterion (BIC). The best model included only burn status and species as fixed effects, and focal ID as a random effect (M1). I then compared this model to a null model (M2) which included only species as a fixed effect and focal ID random effects. The sample size of each model was 1143 handling events across 21 unique individual IDs (including all known adults and subadults, and three focal observations among unidentified adults).

2.4 Results

2.4.1 Fire's effect on search: encounter rates

Fire appears to exert variable impacts on encounters among the different prey types. Encounters for two types of prey were significantly ($P > 0.05$) positively impacted by burning, these include leaves and invertebrates (Figure 2.2, Table 2.3). Encounters for other categories were not positively improved by burning. However, most primate foods were located in trees and shrubs above-ground and did not come in direct contact with fire. Of the terrestrially available prey types, two out of three (invertebrates and leaves) showed significant improvements. Improved encounters with leaves were almost certainly driven by the emergence of new regrowth approximately 4 weeks postburning. It is likely that the emergence of the new shoots also strongly influenced the distribution of insect prey as many of the invertebrate species targeted by the vervets regularly consume shoots and grasses.

Fire can act as an invertebrate magnet, drawing insects into burned areas and aggregating them in spatially bound patches. When total time spent in handling events is compared across subjects, 20% was allocated to handling invertebrates in burned areas compared to only 11% in unburned areas. However, invertebrate foraging efforts were not consistent through time. This may be because fire can act on the distribution of insects in several temporally distinct phases:

· immediately postfire, immobile invertebrate prey such as grubs and larvae that have been cooked in the flames remain, their carcasses are easily retrieved by foragers quickly moving into the freshly burned landscape (Bouwman and Hoffman 2007). Alternately, mobile prey fleeing from fire may be stunned or immobilized by the smoke and flames making their capture easier (bee smoking is a common honey procurement strategy among human foragers worldwide).

· within the first week of fire, invertebrate prey may flee to unburned refugia within the broader landscape of the burn. Aggregated here, they may be easy targets for foragers (Jaffe and Isbell 2009).

· following primary regrowth (4-20 weeks depending on burn season and habitat), invertebrates may repopulate burned areas, feeding on nitrogen-rich new shoots (Swengel 2001; Moya-Raygoza and Larsen 2014). As the new growth attracts invertebrates, insect consumers may be drawn in as well. After new shoots have grown, invertebrate populations stabilize.

· long-term effects of fire on ant populations show that in some habitats, landscape burning at a 3 year interval leads to more abundant and diverse ant populations (Manwaring et al. 2015).

Although I did not observe any significantly positive changes in gum encounters, this is surprising especially since the profitability data reported below indicate that gum provides the highest return rate of any of the vervet food types (Table 2.1 and Figure 2.3), and detailed chemical analyses of *Acacia karoo* gum (the preferred gum producing species) show the substance to consist primarily of carbohydrates (Bearder and Martin 1980). Because of its high energetic yield, gum should be sought by vervets over other prey types. At present, data on exudate flow in *Acacia* species postfire are unavailable (Orians and Milewski 2007). However, research on North American pine species highlight the relationship between exudate production and fire noting that resin flows in Ponderosa pine (*Pinus ponderosa*) are significantly higher following a burn (Perrakis and Agee 2006). While further research must be done to quantify the response of *Acacia* species to fire, if

they exhibit a similar physiological response to Ponderosa pines, I expect increased encounters with their gum. Perhaps analyses were unable to detect changes in gum production and encounters because gum is quickly depleted upon discovery and after a patch is depleted a forager may have to wait for several days for the exudate to appear again. Finer grained data may be necessary to detect this subtle, but potentially important shift.

2.4.2 Fire and handling: prey profitabilities

The effect of fire on profitability appears negligible (Figure 2.3). Postencounter returns did not significantly differ in burned and unburned areas in the model (M1; P=0.13826). When the full model (M1) was compared to the null model (M2), which did not include burn as a predictor variable, no significant differences in fit were detected (P= 0.1326). While burn status did not affect the outcome of the model, the mean profitabilities of several prey types were higher in the burn (fruit: unburned mean = 0.122 ± 0.081 [SD]; burned mean = 0.125 ± 0.061 [SD]; leaves: unburned mean = 0.042 ± 0.026 [SD]; burned mean = 0.047 ± 0.033 [SD]; USOs: unburned mean= 0.082 ± 0.082 [SD]; burned mean = 0.091 ± 0.071 [SD]). However, data were widely dispersed negating any meaningful distinctions. I nominate several issues relevant to detecting postburn energetic shifts below, and reconsider the expectation of improved postencounter returns for vervets.

First, many vervet resources occur high in tree branches, and only a limited subset will ever be directly impacted by fire's flames. Thus, only changes in profitability (due to decreased time spent in handling events) for those resources within reach of flames should be expected. These may include sessile terrestrial resources such as USOs, slow and/or immobile invertebrate prey, and fallen fruits and seeds, each of which may have become cooked on the ground surface during the fires. However, cooked resources are quickly depleted by competitors. For example, avian species, which are typically the first to arrive at a newly burned patch, are attracted to the cooked and charred fruits, seeds, and insects exposed after the removal of ground cover. Fork-tailed drongos, lilac-breasted

rollers, and grey hornbills are known to exploit burned areas until the abundance of recently deceased and fleeing insects is exhausted (Bouwman and Hoffman 2007). Second, limited observations of burnt food consumption and a lack of cooked samples for energetic analysis hampered measurement of changes in the profitabilities of cooked foods. Potential changes in bionutrient availability of cooked resources are systematically underestimated (for examples of physiological and chemical changes caused by cooking see: Kataria et al. 1989; Clemente et al. 1998; Boback et al. 2007; Carmody and Wrangham 2009; Carmody et al. 2011; Ee et al. 2011; Groopman et al. 2014; Zink et al. 2014). Investigations of the specific changes to nutrient availability via cooking carried out in controlled laboratory settings (like those cited above) may be one of the only ways to quantify changes in profitabilies for cooked foods.

2.5 Discussion

Where natural and/or anthropogenic burning are common, primatologists have often observed their subjects using burned areas in novel and unexpected ways (for a summary see: Chapter 1; Herzog et al. 2014). However, without quantitative data to compare the foraging behavior of primates in burned and unburned areas, we are left to wonder, "what's fire got to do with it?" Data reported here show that fire improves encounters with new grasses and invertebrates. This observation is not entirely new, human hunters have long used fire as a tool to attract herbivores into favorable locales well aware of the appeal of new shoots to grazers (Fisher 1948; Hall 1984; Lewis and Ferguson 1988; Bowman et al. 2001). Fire ecologists too have noted this relationship, and termed the draw of herbivores to the nitrogen-rich new shoots that emerge after a fire the "magnet effect" (Van de Vijver et al. 1999; Sensenig et al. 2010). This "magnet effect" draws grazers away from unburned areas, and into recently burned ones (Archibald et al. 2005). Vervets would hardly be considered browsers, but like grass-eating ungulates, they were also drawn to the nutrient dense regrowth. In this study, and others among the same population (Barrett 2009), vervets only infrequently foraged on grasses prior to burning,

even new shoots. However, their increased likelihood of pursuing leaves in the burn indicates that burning alters the energetic value of the shoots (i.e., increases nitrogen values) or decreases the costs of detection, or both.

The influx of invertebrates to these stabilized patches aggregates them there (Swengel 2001; Moya-Raygoza and Larsen 2014), and likely facilitates increased encounters between invertebrates and their predators. When readily available, invertebrates supplement and even supplant other primate foods, a pattern documented even among primates that only occasionally consume insects (O'Malley and Power 2012; Isbell et al. 2013; Rothman et al. 2014). It should come as no surprise, then, that much of the available literature detailing primate behavior in burns describes opportunistic insect hunting (Harrison 1984; Berenstain 1986; Jaffe and Isbell 2009). Similarly, vervets in the present study shifted to an invertebrate-centric foraging strategy in burned savanna. Subjects spent nearly twice as much time handling invertebrates in burned areas than they did in unburned habitats. This increase is strongly suggestive of the pull that increased encounters with invertebrates had in influencing foraging decisions in the burn. While previous research suggested that vervets were primarily drawn to burned areas to take advantage of immediate alterations in invertebrate prey distributions (Jaffe and Isbell 2009), I did not observe this pattern. Rather, vervets in this study appear to have been drawn into burned areas only after they became repopulated by invertebrates. However, because the fire-related behavior of mobile prey is shaped by unique features of the microhabitats in which burns occur, we should expect different timeframes of use in different habitats. Regardless of the timing of invertebrate fluctuations, search improvements to this key subset of vervet prey were the likely motivation for postburn foraging range expansions previously described among this population (Chapter 1; Herzog et al. 2014).

Finally, the preference for burned habitats may be multidimensional. Jaffe and Isbell (2009) suggest that burned areas offer primates an additional benefit in the form of reduced predation. They note that primates foraging in burned areas have an increased

ability to detect predatory threats where reduced ground cover improves overall visibility. At present, only limited work has been done on the response of predators to fire. The outcomes indicate that lions (*Panthera leo*) avoid hunting in burned areas despite the fact that herbivore prey are drawn to them (Eby et al. 2013). Given this supportive data, future research involving the behavioral responses of a larger suite of primary primate predators to fire is warranted.

From chimpanzees to macaques and vervets, primates spanning the Old World clades have been observed foraging in burned habitats, often extracting freshly cooked resources (Harrison 1983; Harrison 1984; Berenstain 1986; Armelagos 2010). The effect may not be so favorable for species dwelling in settings not adapted to regular fire or for primates with highly constrained diets (Berenstain 1986; O'Brien et al. 2003). Vervets inhabit a wide range of environments, and it is possible that advantages for exploiting novel resources in varying contexts underlies the behavioral flexibility that enables them to take advantage of foraging opportunities postfire (Chapter 1; Jaffe and Isbell 2009).

The apparent benefits, and growing evidence of fire-use among Old World primates suggest a likely precursor to and foundation for the obligate pyrophilia that evolved in our own lineage (Pruetz and LaDuke 2010; Parker 2014; Parker et al. 2015). Direct information about hominin plant use (cooked or raw) is almost nonexistent in the archaeological record, so hypotheses regarding types of foods consumed and processing strategies cannot be easily tested by that line of evidence. Because optimal foraging models track a simple currency directly related to evolutionary fitness, they provide a means to explore questions about diet in our deep past (Kurland and Beckerman 1985; Hawkes and O'Connell 1992; O'Connell 1995; O'Connell et al. 1999; O'Connell et al. 2002; O'Connell 2006; Griffith et al. 2010; O'Connell and Allen 2012; Sayers and Lovejoy 2014; Parker et al. 2015). More systematic observations of our evolutionary cousins around fire and burned landscapes can prompt investigators interested in the question of hominin fire use to consider the many and varied ways in which fire may have impacted the foraging opportunities of hominins as they moved into expanding, fire-prone savannas.

Table 2.1. Prey species nutrient and energetic values

Prey species	Prey type	In burn	ME_l/ dry g	%OM	%CP	%NDF	%Fat	%Ash	g per bite	ME_l/ bite
Acacia caffra	Seed	+	3.246	55.1	21.7	20.4	2.2	4.0[a]	0.040	0.130
Acacia karoo	Seed	+	3.227	58.8	18.5	20.2	1.8	4.2[a]	0.033	0.106
Acacia nilotica	Seed	+	3.180	68.4	8.4	21.0	1.5	4.2[a]	0.125	0.399
Acacia robusta	Seed	+	3.055	60.4	15.0	23.3	0.6	4.2[a]	0.050	0.153
Acacia tortilis	Seed	-	3.184	58.4	19.5	20.2	1.3	4.5[a]	0.039	0.124
Bridelia molis	Fruit	+	2.784	55.2	4.3	37.8	2.1	4.0[b]	0.258	0.718
Celtis African.	Fruit	-	3.841	62.7	12.1	15.8	8.7	1.2[b]	0.080	0.307
Chaet. aristata	Fruit	-	3.582	53.4	11.6	25.0	9.4	1.0	0.038	0.135
Comb. zeyheri	Fruit	+	3.691	63.3	9.1	11.7	5.2	4.0[c]	0.364	1.344
Euclea crispa	Fruit	-	2.868	59.5	2.9	34.9	2.0	0.7[b]	0.039	0.112
Ficus burkei	Fruit	-	2.898	59.7	6.7	31.6	1.4	2.0[b]	0.041	0.119
Grewia flaves.	Fruit	+	2.639	57.5	4.3	36.8	0.8	3.2[b]	0.225	0.594
Gum[*]	Gum	+	3.535	86.0	1.8	10.8	0.4	2.8[d]	0.375	1.325
Invert.[†]	Inv.	+	3.566	43.3	27.7	20.2	8.3	3.8[d]	0.250	0.892
Kalan. lanceol.	Leaf	+	3.143	62.3	6.2	28.0	2.8	0.7	0.083	0.262
Mimos. Zeyheri	Fruit	-	2.818	62.9	2.6	33.2	0.6	1.6[b]	0.405	1.141
Olea europea	Fruit	-	2.810	58.9	2.6	35.7	2.1	1.5[e]	0.138	0.388

Table 2.1 Continued

Pap. capen.	Fruit	-	3.852	50.2	6.9	26.4	15.9	0.7[b]	0.079	0.304
Rhus leptod.	Fruit	-	2.802	57.6	6.0	34.1	1.7	2.6[b]	0.027	0.075
Rhus pyroid.	Fruit	-	3.263	71.2	6.3	20.4	1.4	2.6[b]	0.025	0.082
Sclero. birrea	Fruit	-	3.311	73.6	4.4	18.9	2.3	3.8[b]	0.438	1.450
Unk. grass)[§]	Leaf	+	2.552	53.0	8.2	37.3	0.9	5.0	0.120	0.306
USO (*Romulea* sp.)[‡]	USO	+	3.657	-	-	-	-	-	0.330	1.207

ME1= Total metabolizable energy per 1 gram prey item; OM = Organic Matter; CP = Crude Protein; NDF = Neutral Detergent Fiber.

[a] (Aganga et al., n.d.), b (Wehmeyer, 1986), c (Nakagawa, 2003), d (Isbell et al., 2013), e (Zamora et al., 2001)

[*] Composite of three species: *Acacia karoo*, *Acacia tortilis*, and *Combretum zeyheri*

[†] Composite of three species: *Nephila senegalensis*, *Zonocerus elegans*, and *Crematogaster* spp.

[‡] Data from Bennett and Jarvis, 1995.

[§] Research shows increased nutrients in postfire regrowth (Van de Vijver et al., 1999); we therefore estimated a relatively high ash content for this sample.

Table 2.2. OFT formulas

	Measure	Equation	Variables
ME_1	Total metabolizable energy per 100 grams prey item (low fermentation)	$ME_1 = (4\ x\ \%TNC) + (4\ x\ \%CP) + (9\ x\ \%L) + (.543\ x\ \%NDF)$	TNC Total Nonstructural Carbohydrates CP Crude Protein L Lipids NDF Neutral Detergent Fraction
ME_{1b}	Metabolizable energy per bite	$ME_{1b} = ME_1 \times \left(\frac{g_i}{b_i}\right)$	g_i grams per prey item b_i Bites per prey item
IR	Ingestion rate: mean number of bites per handling event (seconds)	$\text{IR} = \frac{\sum b_p}{\sum h_p}$	b_p total number of bites per handling bout h_p time handle per bout (seconds)
E_i	Energy ingested per handling bout	$E_i = ME_{1b} \times b_p$	

Table 2.3. Summary of negative binomial regression models. Models illustrate the effect of search time and burn on encountering resources.

Prey Type	Variable	Estimate	SE of Estimate	Pr(>|t|)
Fruit	Intercept	-2.703	0.209	<0.0001***
	Search time	0.001	0.001	0.101
	Burn	-0.062	0.262	0.813
Gum	Intercept	-1.761	0.223	<0.0001***
	Search time	0.002	0.001	0.000***
	Burn	0.301	0.252	0.232
Invertebrate	Intercept	-1.058	0.134	<0.0001***
	Search time	0.002	0.000	<0.0001***
	Burn	**0.369**	**0.145**	**0.011***
Leaf	Intercept	-3.549	0.376	<0.0001***
	Search time	0.001	0.001	0.136
	Burn	**1.176**	**0.389**	**0.002****
Seed	Intercept	-3.070	0.242	<0.0001***
	Search time	0.001	0.001	0.349
	Burn	-0.213	0.313	0.493
USO	Intercept	-2.607	0.323	<0.0001***
	Search time	0.003	0.001	0.001***
	Burn	0.029	0.372	0.938

* $P < .05$. ** $P < .01$. *** $P < .001$. Positive statistically significant results for burn variable shown in bold.

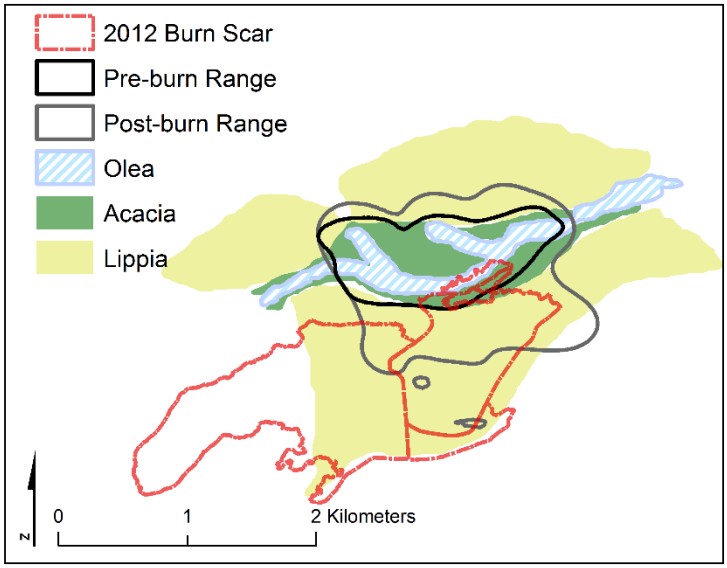

Figure 2.1. Map shows the distribution of plant communities (*Olea europea* woodland, *Lippia javanica* shrubland, and *Acacia* woodland) in and around Donga troop pre- (outlined in black) and postburn (outlined in dark grey) home ranges. The 2012 fire scar is also depicted (dashed red line) to highlight the extent of *Lippia* and *Acacia* burned.

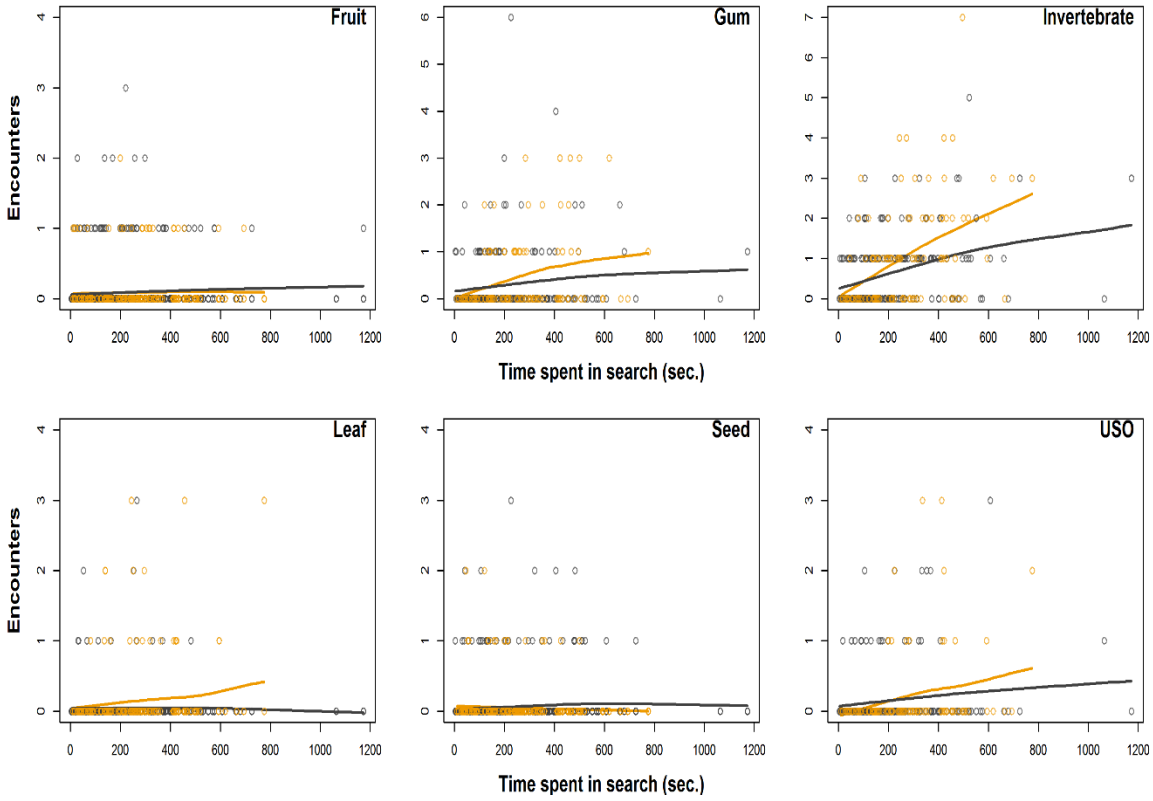

Figure 2.2. Scatterplots showing encounters against the amount of time spent in search for each prey type. Orange dots represent encounters in burned habitats, encounters in unburned habitats are shown in grey. Lines depict smoothed loess curves (derived from models estimated separately for burned and unburned conditions) for burned (orange) and unburned (grey) data.

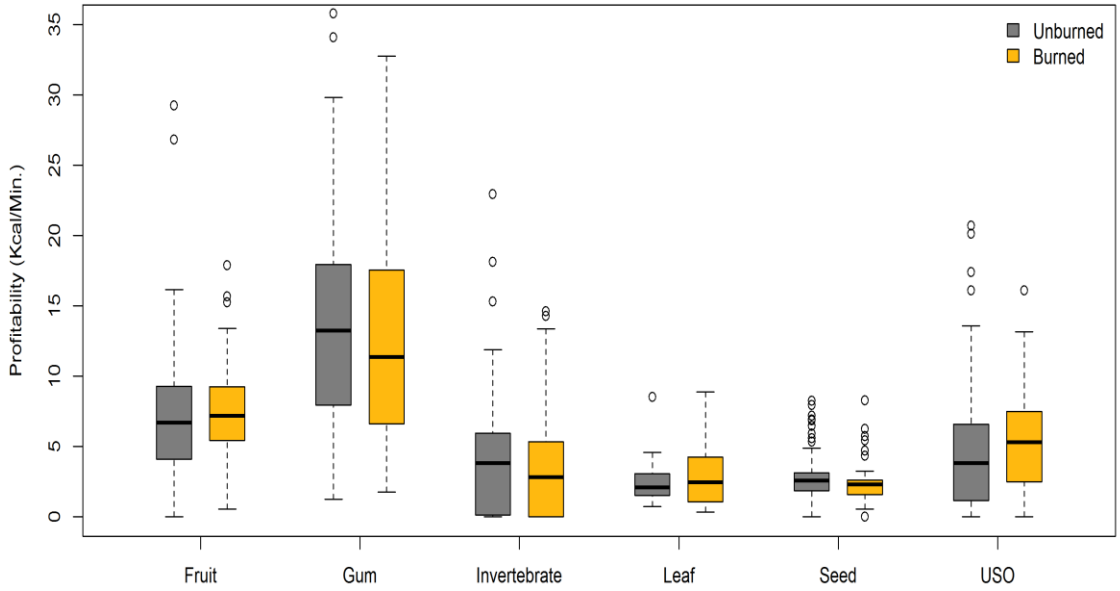

Figure 2.2. Average postencounter prey profitability per prey type in unburned (grey, left plot) and burned (orange, right plot) conditions. Whiskers represent a 95% confidence interval and circles represent outliers.

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CHAPTER 3

FIRE'S IMPACT ON THREAT DETECTION AND RISK PERCEPTION AMONG VERVET MONKEYS

3.1 Abstract

We now know that burning shapes the spatial behavior of primates, but the extent to which burning alters the perceived threat of predation is unknown. In this paper, I study the behavioral responses of vervet monkeys (*Chlorocebus aethiops*) following controlled burn events in order to evaluate whether vigilance was reduced in fire-altered landscapes. I hypothesized that subjects would respond to the elimination of ground cover by exhibiting fewer predator specific vigilance behaviors (bipedal scans, alarm calls, flight). To test this hypothesis, I compare the percentage of time dedicated to various forms of vigilance across different habitats and burn conditions. Results show significant variation in the degree and form of vigilance between habitats. Burning also significantly decreases all forms of vigilance across all habitats. I conclude by describing the ways in which burning creates microhabitats where, relatively free from the threat of dangerous snakes or larger carnivores, primates show less risk averse behavior.

3.2 Introduction

Much has been written on the antipredator strategies of primates in general (Anderson 1986; Isbell 1994; Hill and Dunbar 1998; Stanford 2002; Zuberbühler and Jenny 2002; Gursky-Doyen and Nekaris 2007; Miller and Treves 2007; Hart and Sussman 2009); and specifically on vervet monkeys (Seyfarth et al. 1980; Cheney and Seyfarth 1981;

Baldellou and Henzi 1992; Enstam 2007; Willems and Hill 2009; Makin et al. 2012). However, few researchers have investigated the ways in which fire-altered landscapes shift the predator/prey dynamic (but see: Ogen-Odoi and Dilworth 1984; Eby et al. 2013; Green et al. 2014). In one of only a few publications documenting primates' response to fire, Jaffe and Isbell (2009) report significant changes in the ranging behavior of a population of vervet monkeys (*Chlorocebus aethiops*) after a natural fire. They attribute the alterations to two phenomena. First, that subjects may have been able to travel more effectively because burns eliminated ground cover, enabling them to detect obstacles and better navigate terrain, facilitating faster and further movement. Second, the reduction in ground cover allowed vervets to detect predators at greater distances, lowering their perception of risk and enabling them to move into previously dangerous savanna settings.

To better understand the behavioral responses of vervets to postburn predatory threat, we must first examine general patterns of vigilance behavior within this species. Vervets live in multi-predator environments associated with various types of risk, and like all animals under such constraints, modify their distribution and behavior in response to these threats (Lima 2002; Willems and Hill 2009; Coleman and Hill 2014). The vigilance behavior of vervets has been especially well studied because of their unique vocal repertoire, which contains easily identified threat-specific calls. The most common and acoustically distinct calls are attributed to leopard, snake, or avian predators; but, other calls for minor predators and baboons/unfamiliar humans can also be distinguished (Struhsaker 1967; Seyfarth et al. 1980; Cheney and Seyfarth 1981; Owren and Bernacki 1988). Alarm call fidelity is high and appears consistent across the geographic range of vervets leading researchers to conclude that a deep and consistent history of threat from each of these predator guilds has been a selective force shaping call structure (Price 2013). Of vervets' common predators, leopards (*Panthera pardus*) are responsible for the majority of observed and suspected predation events (Isbell 1990; Isbell and Young 1993; Enstam and Isbell 2002). Leopards hunt by stealth/ambush, using ground cover to approach prey undetected. Rates of success decrease after detection. Therefore, the closer

one can get to its target the better the odds of success (Rice 1981; Bothma et al. 1994; Hayward et al. 2006). The probability of a successful kill is highest in areas with intermediate ground-level plant growth (Balme et al. 2007), which explains why leopards are seldom observed hunting in open habitat (Bailey 1993; Hayward et al. 2006). When leopards do hunt in open habitat, they do so at night (Bailey 1993). In settings with greater cover, attacks occur both nocturnally and diurnally (Cowlishaw 1994; Hayward et al. 2006). Given these proclivities, vervets face the greatest risk from leopards in areas of mixed vegetation, and in habitats with discontinuous, smaller, trees where the options for vertical flight are fewer.

Threats from other common vervet predators including serpents, birds, small mammals and other primates occur in both closed canopy and open settings (Hart and Sussman 2009; Headland and Greene 2011), and primates' perception of these threats ultimately shape their ranging behavior (Willems and Hill 2009). Although snakes are rarely reported to prey on primates (for some examples see: Isbell 1994; Isbell 2006; Hart and Sussman 2009; Headland and Greene 2011), snake bites are often deadly (Isbell 2006). Snakes pose the greatest threat in areas of dense vegetation, or heavy ground cover, where they blend easily and are difficult to detect. Primary African avian predators (martial eagles, crowned eagles, and owls) are not known to target terrestrial primates, but for canopy-dwelling primates can pose a serious threat. For example, in Kibale Forest, Uganda, canopy-dwelling monkeys accounted for 80-90% of crowned eagle diets (Struhsaker and Leakey 1990; Sanders et al. 2003). Vervets face some pressure from avian predators, but because they spend time foraging terrestrially and in low-growing bushes and shrubs, are less likely to be targeted (Isbell 1994). Avian predators pose the greatest threat when vervets move along terminal branches or travel higher in the forest canopy. Finally, opportunistic attacks from baboons do occur, especially when troops are encountered unexpectedly. Where data on predation exist, baboons can account for up to 50% of all vervet fatalities and vervets can comprise up to 22% of baboons' vertebrate intake (Hausfater 1976; Cheney and Seyfarth 1981). However, baboons generally target

immatures. As a result, adults only infrequently alarm call in their presence (Cheney and Seyfarth 1981). When possible, vervets avoid contact with baboons by altering their direction of travel when a baboon alarm call is made, or when nearby baboon troops are detected (Cheney and Seyfarth 1981).

In areas where vervets experience heightened risk (ground cover is dense and/or grasses are tall), a wildfire can quickly transform favorable hunitng conditions into relatively poor ones. Devoid of ground cover, burned settings lack ambush opportunities for many vervet predators. Recent research shows that lions (*Leo panthera*) avoid burned areas despite the fact that herbivore densities are often higher there (Eby et al. 2013). Similarly, at a field site in Uganda, two large carnivores, leopards and civets (*Civetticis civetta*), disappeared entirely from burned habitats despite a 300% increase in an appealing prey item, savannah hares (*Lepus crawshayi*) (Ogen-Odoi and Dilworth 1984). Snakes also pose a threat to vervets, but it appears they too avoid burned areas. A recent study shows that snakes face greater risk in open settings; predation attempts on artificial snake models were significantly higher in recently burned settings as compared to predation attempts in similar but unburned areas (Wilgers and Horne 2007).

If, as the above data suggests, fire does act to deter vervets' primary predators and threats, burned areas may be particularly appealing. Here, I test Jaffe and Isbell's (2009) hypothesis that fire-mediated differences in predator behavior alter vervets' risk in burned landscapes. Using a set of spatial and behavioral data collected both before and after controlled burning events, I evaluate the form of alarm calls and other vigilance behaviors as they relate to the detection of both predators, threats, and antagonistic neighbors. Postfire, the behavioral markers of perceived risk were lower in burned areas suggesting that burning reduces that threat of predation thereby enabling vervets to forage in areas otherwise too dangerous.

3.3 Methods

3.3.1 Study population and behavioral data collection

The research detailed here was conducted among a troop (n=23) of savanna-dwelling vervet monkeys at Loskop Dam Nature Reserve, SA. Portions of the primates' home range as well as surrounding savanna were burned during the controlled burning regime of 2012. Behavioral observations among this study population were conducted for approximately 90 days prior to burning, and for 90 days after. The home range of the study troop can be broken into three primary vegetation communities: *Olea europea* subsp. *africana-Rhus leptodictya* woodland, *Lippia javanica-Loudetia simplex* shrubland/grassland, and *Acacia nilotica-Acacia caffra* woodland. The *Olea* vegetation community grows within and along drainages and is characterized by tall (~20 m) closed canopy vegetation, and sparse ground-level cover plants. The bordering *Acacia* and *Lippia* vegetation communities are typically less dense, with little or no closed canopy. In these habitats, tall grasses and small shrubs create significant ground cover and limit ground-level visibility. In *Acacia* habitats low-growing trees (<5 m) are common, while the *Lippia* habitat is relatively tree sparse with a mix of both taller (>8 meters) and low-growing trees.

Vervet behavioral observations included both scan samples and focal follows (Altmann 1974). Scan samples were conducted in 15 minute intervals and focal follows were conducted for a duration of 20 minutes once every hour. In total 694 focal follows (232 hours of observation), and 2640 scan samples were collected using Trimble GPS units and Cyber Tracker (www.cybertracker.org) software. Behavioral information collected during each focal follow included: behavior, habitat (*Acacia*, *Lippia*, or *Olea*), subhabitat (closed canopy, dispersed trees, shrubs and bushes, grasses, altered/disturbed), and burn status (unburned, newly burned, primary regrowth, secondary regrowth). Behavior was further broken into the following categories: 1) foraging, which includes both the pursuit and handling of food items; 2) movement, whether climbing, walking, or running; 3) affiliative and antagonistic/agonistic social behavior; 4) social or predatory vigilance including fleeing, scanning, and attacking or vigilance directed at an unknown threat; and

5) rest. Like vervets at other field sites, those observed in this study produced three acoustically distinct alarm calls (leopard, eagle, and snake). Subjects also used a fourth call, often directed at either baboons or human activity, which appeared to be a more generalized threat vocalization. When field researchers were unable to detect the cause of vigilance behavior, the call structure of adults (juveniles and infants often misuse calls) was used to help determine the type of threat involved. Vigilance behavioral descriptions were amended if the cause of the vigilant behavior was detected after the scan or focal had taken place. Only bipedal scanning events were scored as vigilance, as other forms of scanning were too ambiguous to attribute to threats or predators alone. Vigilance data analyzed here include social vigilance, or agonistic/antagonistic behaviors directed toward neighboring troops or supernumerary males based on the reasoning that if burning can improve the detection of neighboring troops, fewer costly clashes should occur.

To quantify vigilant behaviors I use a combination of both focal and scan sample vigilance data. I compare differences in percentage of time spent in vigilance, and type of vigilant behavior between habitats and across burn conditions. To estimate the proportion of behavior related to vigilance, I tabulated all of the occurrences of scan, flee, or alarm call. I then divided that number by the total number of behaviors observed for each habitat (*Olea*, *Acacia*, and *Lippia*) and burn status (burned, unburned).

3.4 Results

3.4.1 Observed predators and threats

During the 2012 field season we directly detected (via vocalizations and sightings) several vervet predators and/or threats including: baboon (*Papio ursinus*), black mamba (*Dendroaspis polylepis*), leopard, puff adder (*Bitis arietans*), rock python (*Python sebae*), serval (*Felis serval*), one unidentifiable avian predator, and several unidentifiable snakes (Table 3.1). Other potential predators occur in the Reserve, but were not observed during the 2012 field season. They include: African wild cat (*Felis lybica*), black backed jackal

(*Canis mesomelas*), caracal (*Caracal caracal*), marital eagle (*Polemaetus bellicosus*), and Nile crocodile (*Crocodylus niloticus*). The only predators/threats observed while vervets were within burned areas were a troop of baboons and a bird of prey (for behavioral response see: Table 3.1). All other observations of predators/threats occurred in unburned habitats.

No predation events were directly observed during the course of fieldwork, and during that time no animals disappeared from the study troop. However, I speculate that predation attempts did occur outside of observation. On two separate occasions adult males acquired wounds indicative of attacks (one with a wide slash mark on haunches, and another with a wide gash [bone visible] down a possibly broken radius/ulna) after observers left them at sleeping sites for the night. We attributed the wounds to predator attacks because of the nature of the wounds and because nocturnal attack by predators are common and often occur near sleeping sights. Antagonistic nighttime interactions with neighboring troops have not been reported for vervets. However, nighttime attacks from in-group males have been observed among both captive and wild chimpanzees (J. Pruetz, pers. comm.) thus, this possibility cannot be ruled out. Both males healed from their wounds, although one was debilitated for approximately 1 week after, and never regained full mobility in the injured arm.

3.4.2 Vigilance events

Vigilance events were relatively rare during the study period. Postfire, vigilance events occurred in 95 of 426 (22%) focal follows in unburned habitats. Within burned habitats 22 of 111 (20%) focal follows documented an instance of vigilant behavior. Vigilance events were even less frequent during scan samples, making up less than 1% of all individual observations (324 out of 14,824 individual observations during postfire scans in unburned areas, 37 of 2,550 individual observations in burned areas).

Each of the three habitats used by vervets poses a different type of threat, and requires different mechanisms for avoiding potential predators. In *Olea* habitats, tall trees

provide a safe refuge from terrestrial ambush predators, but, also provide ample concealment for those predators. In open *Lippia* grassland, predators may be detected at greater distances, however, safe refuges are much more difficult to access and subjects may be more frequently exposed. Shrubland *Acacia*, represents a mixed habitat with a thick understory and both patches of canopy and stretches of grass. To explore the differences in vigilance between these varied habitats I compared the total number of vigilant events recorded and the percentage of those events represented by different forms of vigilance.

Results show that the form of vigilance behavior differs significantly both between habitats and within burned and unburned conditions of a given habitat (Figure 3.1). A Tukey's Honest Differences test showed that regardless of burn status (unburned or burned), the percentage of observations recording vigilance events in each habitat differ significantly from one another (P <.05). The structure of vigilance behavior (i.e., the portion of all observed instances of vigilance that are alarm calls) also differed significantly (P <.05) between habitat types, regardless of burn status. When I compare behavior across burn status (burned vs. unburned areas within in habitat type), differences in both the frequency and structure of vigilance behavior become even more pronounced. Kruskal Wallis rank sum tests show significantly fewer vigilance events occur in burned areas (chi-squared = 20.826, df = 1, P = <0.0001) and that a smaller percentage of those events are alarm calls (chi-squared = 7.251, df = 1, P = 0.007). In sum, vigilance strategies differ across habitats, but more importantly, burning appears to significantly decrease all types of vigilance regardless of habitat type.

3.5 Discussion

Previous research has emphasized predation as a key force shaping features of primate morphology, cognition, sociology, and ranging behavior (Alexander 1974; van Schaik 1983; Anderson 1986; Isbell 1994; Isbell 2006; Hill and Weingrill 2007; Zuberbühler 2007). However, predation's role in each of these aspects of primate life is difficult to

quantify, partly because data on rates of predation and vigilance behavior are notoriously difficult to acquire (van Schaik 1983; Isbell 1994; Hill and Dunbar 1998; Enstam 2007). We now know that the presence of observers alone can alter the behavior of both predators and prey. For example, samango monkeys spent more time in ground-level patches when accompanied by a human than when unobserved. Researchers detected the difference using camera traps and attribute the shift in habitat use to the monkeys' ability to recognize the reduction of risk created by the presence of an observer (Nowak et al. 2014). Consistent with these findings, others have quantified the success of ambush predators, and found it to be lower when researchers accompany primates (e.g., vervets in Amboseli: Isbell and Young 1993). Another difficulty in quantifying perceived or real risk is accurately identifying vigilant behavior and predation events (Enstam 2007). Many primates engage in vigilance that is undetectable to the observer, leaving observers to focus on overt displays, while undervaluing more nuanced risk avoidance. In addition, study animals may come and go from populations, often overnight. Without direct observation of predation events, the frequency of predation-related deaths that is necessary to assess risk remains unknown (Hill and Dunbar 1998). Finally, even when predation is documented, and risk is evaluated, the extirpation of extant predators largely undercuts historic (and predictions about prehistoric) rates of predation. In spite these limitations, the results presented here confirm the general importance of predation in shaping vervet behavior and identify marked changes in vigilance across habitats and especially when burned.

For vervet monkeys, access to refuges, tree height, and amount of vegetative cover are the primary components shaping actual and perceived risk (for a summary of primary data see: Enstam 2007). Because savannas (like the *Lippia* habitat in the present study) provide fewer refuges and potentially house more predators (Treves and Palmqvist 2007), predation risk there has been assumed to be higher there than in closed canopy habitats (akin to the *Olea* habitat here). While this is true of savannas comprised of tall grasses (which provide cover for terrestrial stealth predators), short grass savannas may actually

be safer than other more densely vegetated habitats (Isbell 1994). In more open landscapes, terrestrial predators are detectable at greater distances, decreasing their odds of a successful ambush. Though vervets may become more visible to avian predators in open/burned settings, our results indicate that the advantage of seeing terrestrial predators outweighs advantages to the avian predators better able to detect them.

In the study area, *Acacia* habitats were most dense, included substantial ground cover, and contained only short, dispersed trees. Therefore, this habitat likely provided the best ambush opportunities for predators. Like other vervet populations that employ flexible antipredator strategies based on the structure of the habitat where the threat occurs (Enstam 2007), subjects exhibited the greatest proportion of vigilant behavior here. In the *Lippia* grassland/savanna setting vervets rarely used alarm calls. In these open settings, where options for refuge were limited, subjects employed more cryptic strategies (i.e., fleeing and scanning). These results are similar to those reported by Enstam and Jaffe (2002), who found that vervets traveling within the savanna employed anti-predator strategies similar to those of permanently savanna-dwelling patas monkeys (*Erythrocebus patas*).

For ecologically tethered species such as vervets, savanna habitats may be too dangerous to use on a regular basis. Fire can change that by easing the cost of travel (Chapter 1; Herzog et al. 2014), reducing the threat of predation by deterring snakes and felid predators, and creating profitable prey patches (Chapter 2). Jaffe and Isbell (2009) attribute postfire changes in vervet foraging behavior to an increased ability to detect predatory threats in areas with reduced ground cover and greater overall visibility. Deprived of potential concealment, they argue, predators and potential threats are observable at greater distances, necessitating fewer and shorter vigilance events by any given individual. The pattern reported here supports their hypothesis. Postfire, vervets in this study altered their ranging behavior, spending a large portion of time each day traveling terrestrially in the burned savanna (Herzog et al. 2014). Within burned savanna, vigilant behavior represented a significantly smaller portion of all observed behaviors

suggesting subjects felt less at risk there. These results highlight the positive role of fire in alleviating perceived risk, the benefits of which may take the form of improved encounter and return rates for primates able to forage in burned savanna settings (Herzog et al. 2015). Both the reduced risk and improved foraging opportunities should make burning a boon for many savanna-dwelling primates and we should expect members of these populations to take advantage of burned landscapes when and where they occur.

Table 3.1. Direct observations of predators/threats and vervet responses.

Species	Number of obs.	Burn status	Response
Papio ursinus	2	Burned (1)	Alarm calls: indiscriminate Flight: fast terrestrial and/or arboreal movement in opposite direction of baboons
		Unburned (1)	Flight: fast terrestrial and/or arboreal movement in opposite direction of baboons
Dendroaspis polylepis	1	Unburned (1)	Avoidance
Panthera pardus	4	Unburned (4)	Alarm calls: terrestrial predator alarm calls. All adult males, two adult females Alarm calls: indiscriminate. Two subadult males, several juveniles Flight: all individuals moved into high canopy
Unidentified snake	4	Unburned (4)	Alarm calls: snake specific. Flight: subjects moved off ground, into low branches Mobbing: subjects harassed snakes by chuttering at them, moving quickly up and down in branches, and shaking leaves until the threat moved off
Unidentified eagle/raptor	1	Unburned (1)	Alarm calls: avian specific. Flight: subjects moved lower in the canopy

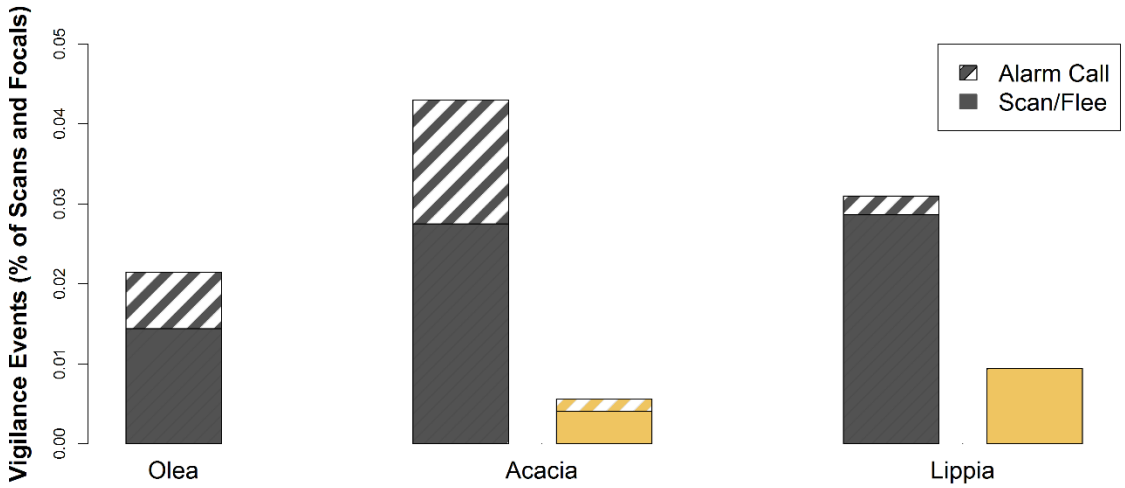

Figure 3.1. Percentage of all focal and scan samples recording vigilance events related to predatory threat (scan/flee and alarm call). Grey bars (left) represent vigilance in unburned areas, orange bars (right) represent vigilance events in burned areas.

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CHAPTER 4

APPLYING A GENERAL THEORY OF BEHAVIOR TO THE ORIGINS OF HUMAN FIRE-USE: LESSONS FROM A NONHUMAN PRIMATE CASE STUDY

4.1 Abstract

Fire use in its many forms is ubiquitous among human populations. However, at present, we know little about how and why humans began using fire. While many have theorized about the emergence of fire use, the behavioral steps themselves left few archaeological traces. Here, I use a primate case study to explore fire-mediated ecological alterations and their effect on ranging patterns, foraging, and predation risk. I hypothesize ways in which these alterations would have favored a fire-centric behavioral strategy in our own lineage. I show that responses to fire among living primates provide a line of evidence that is especially crucial for building evolutionary scenarios of human dependence on fire given the limitations of the archaeological record.

4.2 Introduction

The importance of fire in shaping the behavioral suite unique to our own species has long been recognized (Darwin 1869; Oakley 1956; Stahl et al. 1984; Clark and Harris 1985; Goudsblom 1986). Recently, rigorous attempts to explore the acquisition of fire control and the adaptive alterations that follow have experienced a renaissance. However, progress is slowed by an inability to disambiguate early dates and varying evolutionary scenarios. At present, questions regarding the origins of fire use, like many questions

about the behavioral repertoires of early hominins, are complex, with answers likely a long time coming. As a parallel theoretical debate consider the body of research regarding hominin meat eating that began in the 1980s and continues through the present. The debate pivots between two positions related to the taphonomy of competition and carcass acquisition among hominins. Participants include one set of researchers who argue that a reading of the patterning of bone distribution at early sites, most notably FLK Zinj, suggests selective butchery, high-yield part transport, and ultimately the use of home bases by socially sophisticated hominins (Isaac 1978; Bunn 1981; Bunn et al. 1986). The alternative view proposes that the remains reflect opportunistic scavenging rather than selective hunting (Binford 1981; Potts and Shipman 1981; Shipman 1986). To resolve the debate, some have revisited and reanalyzed the material remains while others have conducted experimental work replicating assemblage patterns and damage morphology (e.g.,: Behrensmeyer et al. 1986; Blumenschine 1988; Marean et al. 1992; Blumenschine 1995; Domínguez-Rodrigo 1997; Selvaggio and Wilder 2001). However, both the interpretive and experimental approaches lack the ability to detect appropriate ecological and evolutionary drivers of the behavior in question. As summarized by O'Connell et al. (1999: pg.465):

> [T]he potential impact [of such work] is limited by the narrow goal of accounting for certain features of the archaeological record (mainly faunal assemblage composition) rather than the larger evolutionary phenomenon of which it is part.

To move forward, O'Connell and colleagues, urged theorists to explore multidisciplinary frameworks. They advocated the use of ecological models to better understand the behavioral strategies dictating patterns in archaeological remains (O'Connell 1995; Bird and O'Connell 2006). Predictions derived from these theoretical models could then be explored via ethnoarchaeological research, experimental archaeology, environmental reconstructions, and comparative studies among living organisms (Blumenschine 1986; O'Connell et al. 1988a; O'Connell et al. 1988b; Lupo and O'Connell 2002; O'Connell et al. 2002; Lupo 2006).

Like the scavenging/hunting debate, scenarios for early fire use also lack definitive archaeological evidence, and like that argument, the timing, type, and structure of early fire use have profound implications for the evolution of our genus. Within the "origins of fire" debate, evidence can be divided into two types. Paleoanthropologists, on the one hand, point to the many physiological and morphological alterations characteristic of early hominins, specifically *H. erectus*, as adaptations to a diet of cooked foods. They argue these adaptations were driven by persistent and committed use of fire from as early as 2.6 million years ago (MYA) (Wrangham et al. 1999; Wrangham 2009; Wrangham and Carmody 2010). Alternately, within the archaeological community, investigators vie for evidence of the earliest detectable hearths (otherwise termed "on site" fires) and use these data as support for the timing and origin of human fire-dependence. Within the archaeological community, one camp places the evidence for controlled use of fire anywhere between 1.7-1.4 MYA (Gowlett et al. 1981; Bellomo 1993; Bellomo 1994; Weiner et al. 1998; Rowlett 2000; Beaumont 2011; Pickering 2012; Gowlett and Wrangham 2013) while others assert a younger age of 350-50 thousand years ago (KYA) (Roebroeks and Villa 2011; Sandgathe et al. 2011a; Shimelmitz et al. 2014). Just as the scavenging/hunting debate was plagued by a lack of ecologically derived predictive models, so too, are the morphological vs. archaeological approaches of the "origins of fire" debate. Without testable hypotheses regarding the behavior of a primate moving from the passive exploitation of burned landscapes to the active manipulation of fire both approaches fail to recognize the larger evolutionary forces at play, and the behavioral and adaptive responses those forces may have generated.

4.2.1 Fire and its role in hominin physiology

Recent publications highlight the potential impact of fire on hominin physiology, some focusing on anatomical adaptations (Wrangham 2009; Wrangham and Carmody 2010), others on cognitive and social processes (Rolland 2004; Burton 2009; Dunbar and Gowlett 2014; Wiessner 2014; Attwell et al. 2015). Here, I summarize the anatomical

adaptationist perspective as their predictions are derived from observed changes in hominin morphology detectable in the paleontological record. Perhaps the strongest proponent of this line of inquiry has been Richard Wrangham. In an influential early paper on the topic, Wrangham et al. (1999) argue that the use of fire for cooking led to the smaller teeth, smaller guts, increased body size, and a decrease in sexual dimorphism observed in early *Homo*. Expanding on the "cooking hypothesis," Wrangham and others have conducted a series of experiments investigating the effects of cooking on energetic extraction (Wrangham and Conklin-Brittain 2003; Boback et al. 2007; Dominy et al. 2008; Carmody and Wrangham 2009; Wrangham and Carmody 2010; Carmody et al. 2011; Organ et al. 2011; Groopman et al. 2014; Zink et al. 2014). Results consistently demonstrate that cooked foods provide increased energetic returns both by denaturing proteins, making them easier to digest and by decreasing the toughness of meat and plant parts thereby decreasing the amount of energy expended on chewing. In concert with these morphological changes, brain size increases and neuronal density rises dramatically (Fonseca-Azevedo and Herculano-Houzel 2012; Pontzer 2012a); a shift supported via expanded energy budgets, a reduction in feeding times, or both. Both scenarios imply the addition of cooked foods to pre *erectus* diets (Navarrete et al. 2011; Organ et al. 2011; Fonseca-Azevedo and Herculano-Houzel 2012). This body of work lends traction to the cooking hypothesis, and supports an early date for fire use. However, little is known about *how* hominins first acquired fire for cooking. At present, the evolutionary scenarios put forth—that fire was first generated by accidental flint sparks or that rambunctious adolescents captured fire by taunting one another with burnt logs—are largely unsatisfying (Parker et al. 2015a; Parker et al. 2015b). Focusing attention on the ways in which fire is manufactured, and the archaeological assemblages of that process, potentially offer a means of pinpointing the origin of some forms of fire-making technology (Sorenson et al. 2014). However, this approach, too, will be limited by the nature of material remains and unfavorable taphonomic processes. Again we are left with the task of identifying an approach that can accommodate the possibility that the earliest

forms of intentional and controlled fire use simply involved the transportation of embers from natural fires (Wiessner 2014).

4.2.2 Archaeological inferences

Archaeology is, by nature, a field of "firsts" and "oldests," and investigations of early fire use are no exception. At present, the debate regarding the antiquity of fire use centers on the validity of early manifestations of fire in the Plio-Pleistocene archaeological record. One of the oldest, and most convincing, dates for hominin fire use comes from Koobi Fora in the Lake Turkana area of northern Kenya, dated to 1.6 MYA. Here use of fire is supported by two lines of evidence. The first are oxidized sediments, which appear "hearthlike" in shape and size. These sediments exhibit much higher levels of magnetic susceptibility than adjacent sediments suggesting they were altered by heat in a way surrounding sediments were not (Bellomo 1994; Bellomo and Kean 1997). Second, phytoliths belonging to several different species are present in the oxidized sediments. If the sediments had been altered by the hot and long process of a single stump burning in a natural fire, such phytolith diversity in the ashy remains would be unlikely. Rather, one would expect an assemblage dominated by microfossils of the parent plant (Rowlett 2000). Two additional contenders for the oldest archaeological evidence of hominin controlled fire include another open-air site in Kenya, Chesowanja, and the Swartkrans cave site in South Africa. Multiple lines of evidence support the antiquity of fire use at these sites. At Swartkrans burnt bone, some of which shows signs of butchery (Pickering et al. 2005), was found in several layers which suggests multiple and controlled uses of fire (Brain 1983). Analyses of the charred bones show that the temperatures at which the bones were burned was too high to have been created by a quick moving grassfire (Brain and Sillen 1988). The evidence for fire at Chesowanja, much like that of Koobi Fora, includes concentrations of baked clay (Gowlett et al. 1981). A detailed taphonomic reassessment of burnt clasts indicated limited postdepositional disturbance, meaning the clasts likely remain near their original location, a tight "hearth like" cluster (Gowlett 1999).

While none of these sites contain what many archaeologists would consider "concrete" evidence of fire—namely hearths—advocates for an early date note the ephemeral nature of open-air cooking fires among contemporary hunters and gatherers, and argue that, in the absence of identifiable hearths, greater attention must be paid to less "concrete" data.

While hearths remain elusive in the early record, an undeniably visible pattern of sustained/increased fire use, characterized by large numbers of burned flints and charcoal lenses, emerges at ~400 KYA across many ecological settings (Karkanas et al. 2007; Stiner et al. 2011; Shahack-Gross et al. 2014; Shimelmitz et al. 2014). This pattern is especially marked in European and Levantine sites, where earlier evidence of fire is very limited. While some argue this uptick indicates a greater degree of controlled use, others contend that archaic hominins living in Europe never mastered fire. These scholars argue that earlier occurrences in the European record represent only "incidental" or "opportunistic" fire use and suggest that the appearance of consistent fire use there is tied to the arrival of modern humans near the end of the Middle Paleolithic period ~50 KYA (Sandgathe et al. 2011a; Sandgathe et al. 2011b). Whether we accept the older, Lower Paleolithic dates, or those from the Middle Paleolithic, both hypotheses can be lumped into the "late control" camp.

If the fire data from Africa is secure evidence of hominin fire use, the "late control" hypothesis would assume that fire knowledge was lost sometime after hominins dispersed to Europe. This seems unlikely given the ubiquity of fire use globally (Scherjon et al. 2015). There are no known human populations, past or present, without some form of fire technology—although data suggested Tasmanians had lost the ability to create fire, direct observations showed that populations had limited mechanisms for fire manufacture but not an absence of its use (Gott 2002; Parker 2014). Underlying fire's pervasiveness are its economic benefits, which we and others argue would have been so strong that abandonment would have been unlikely, especially among hominin populations moving north into cooler and/or less productive biomes (Burton 2009; Wrangham 2009; Parker 2014). Evidence for the presence of fire at Eurasian sites

(Zhoukoudian and Xihoudu: James et al. 1989; Zhoukoudian Rolland 2004; Gesher Benot Ya'Aquov: Alperson-Afil and Goren-Inbar 2010) associated with hominins assumed to have been predecessors of hominins in the "late control" scenario further undermine the argument. Given these objections, the pattern observed in Europe appears to tell a story about a change in the behavioral strategies of fire users, rather than one about fire innovation itself. Taken together, these issues prompt archaeologists to develop criteria for identifying not just the existence of controlled fire but for all possible uses of fire. One method increasingly applied involves the application of refined micromorphological techniques in distinguishing between burned and unburned sediments (Bellomo 1993; Mallol et al. 2007; Pickering 2012; Gowlett and Wrangham 2013). Another, uses environmental reconstructions to tie hominin occupations to local habitat alterations driven by landscape burning (Scherjon et al. 2015). Without multidisciplinary and fine-grained data, the focus remains identifying hearths at the expense of other (and possibly earlier) fire innovations such as landscape modification, off-site food processing, and fire for use in honey gathering. While archaeologists continue to debate the validity of the early evidence for hominin fire use, sometimes with good reason, the limited resolution of archaeological data make absence of uncontested archaeological evidence an insufficient reason to abandon an "early date" hypothesis.

4.2.3 Ecological setting

The full behavioral repertoires of the earliest members of our genus will never be known. What we do know is that in order for any animal to exploit burned landscapes, natural fires must be a common occurrence. In sub-Saharan Africa the C4 grass expansion that began in the late Miocene (from ~7-6 MYA) was almost certainly driven by the occurrence of frequent and cyclical fires (Bond et al. 2005; Sepulchre et al. 2006; Cerling et al. 2011). However, the widespread expansion of very open grasslands, which are especially prone to seasonal burning, likely did not occur until the Late Pliocene/Early Pleistocene (Segalen et al. 2007). Numerous lines of evidence point to increasing

aridification and savanna expansions at or near this timeframe (~3.5 MYA), the effect of which ultimately influenced the structure of mammalian populations in eastern Africa (deMenocal 1995; Vrba 1995; Bobe and Behrensmeyer 2004; deMenocal 2004; Wynn 2004; Feakins et al. 2005; Sepulchre et al. 2006; Cerling et al. 2011). These climatic fluctuations continued in the regions of highest hominin diversity, becoming especially unstable around 2.5 MYA and again from 1.9-1.5 MYA (Trauth et al. 2007; deMenocal 2011; Potts 2012; Potts 2013). Lipid biomarkers from Lake Olduvai indicate pronounced shifts from woodland to open savanna settings mediated by changing levels of precipitation during the later timeframe (Magill et al. 2013a; Magill et al. 2013b). Concurrent with these climatic fluctuations, a new family of fire adapted plants arose suggesting that by 2 MYA the common occurrence of fire had become a selective force among savanna flora, as well as fauna (Maurin et al. 2014). Adaptation to increasingly variable environments have long been assumed to be drivers of human evolution, and it is within the broader ecological context of environmental instability and flux that we place the earliest hominin fire manipulators.

4.3 Primates as models for passive fire use

The goal of this project is to use behavioral data documenting the uses of fire-modified landscapes among a population of nonhuman primates to draw inferences about the earliest use of fire among hominins. Observations of the costs and benefits that landscape fires provide for primates living in fire-prone regions should lead to predictions about likely ancestral responses to landscape fires and so provide the basis for hypothesizing possible archaeological or paleontological consequences of increased fire frequency. Elsewhere we have outlined the ways in which optimal foraging models can be used to systematically quantify changes in foraging opportunities and outcomes (Chapter 2; Herzog et al. 2014; Parker 2014; Parker et al. 2015a; Parker et al. 2015b). Here, I focus on the role of fire as it relates to three issues thought to be critical in the reconstruction of human evolutionary history: 1) establishing foraging niches in a savanna setting, 2)

prey/predator interactions, and 3) hominin dispersals.

4.3.1 Why vervets?

Much has been made of the choice of referential models in creating analogies between the behavior of extinct hominins and extant primates (for a review see: Vaesen 2014). The debate often turns on the relevance of ecological similarity on the one hand, and close evolutionary/genetic relationships on the other. Strong arguments can be made for both. However, as noted by Elton (2006: pg. 26), question matters:

> [B]y exploring the principles that underlie certain types of behaviours in modern primates, inferences about what was possible in hominins under specific conditions can be made (Strum and Mitchell 1987). In some cases the study of apes will provide the most appropriate baseline, but in others certain cercopithecid species will be more informative. The most recent referential models…have avoided the trap of oversimplification by identifying the underlying biomechanical, ecological, or evolutionary principles that influence morphology and behavior.

This research is meant to outline a general pattern of behavior dictated by specific ecological change. Here, I use observations from an Old World cercopithecoid, vervet monkey (*Chlorocebus aethiops*) because this species inhabits an ecological niche similar to that of early hominins, and has been shown to exhibit a propensity for the use of fire-altered landscapes (Jaffe and Isbell 2009; Herzog et al. 2014).

Hominins are characterized by their quick and widespread dispersals and their ability to colonize marginal, or edge, habitats effectively (Cachel and Harris 2003; Wells and Stock 2007; Harcourt 2012; Antón et al. 2014). Vervets also share an affinity for the transitional zones between forests and savanna (Hart and Sussman 2009), and, aside from humans, are one of the most widely dispersed Old World primates (Wolfheim 1983). Consequently, vervet diets are similar to the proposed diets of early hominins—specifically, they are eclectic omnivores targeting a range of canopy and terrestrial resources both vegetable and animal (for a review of vervet diets see: Struhsaker 1967; for hominin diet reviews see: Ungar and Sponheimer 2011; Sayers and Lovejoy 2014). These ecological and behavioral similarities draw our attention to vervets as a proxy for

early hominins, and I surmise that under fire-driven local ecologies the selection pressures working on this extant species may be a useful analog to our own evolution. Other primate referents such as chimpanzees (*Pan troglodytes*) may also provide appropriate analogies, and observations of this species (*P.t. verus*) in a savanna habitat have already revealed compelling fire-related behaviors (Pruetz and LaDuke 2010). Although limited at present, future research focusing on fire's effect on foraging decisions among other savanna-dwelling primates is warranted. Such data would not only complement those reported here, but enrich our understanding of the complex selective pressures shaping the behavior of primates living in close contact with frequent fire.

4.3.2 Vervet behavioral responses to burning

In previous chapters I have quantified the ways in which vervets respond to burning events. These pieces focus on three topics: feeding ecology, risk, and home range expansion. Here, I briefly outline the results of those studies, then use them to generate hypotheses regarding passive fire use in hominin populations.

To quantify changes in foraging opportunities created by fire, I evaluated post-encounter profitabilities and encounter rates in burned and unburned habitats (Chapter 2). Results indicate that burning enabled vervets to more effectively search for some prey items, most notably invertebrates (Figure 2.1). Encounters for invertebrates and leaves were significantly higher in burned areas. Other resources, such as gum, showed positive but nonsignificant trends in encounters postburning. Fire did not appear to alter handing costs, potential explanations for the lack of positive handling improvements is discussed above (Chapter 2).

I also tested the hypothesis that substantial secondary benefits such as reduced perceived predation risk may have shifted primate behavior after fires (Chapter 3). Predation rates for savanna dwelling primates range from 3-15% annually (Cheney and Wrangham 1987); vervet populations fall on the high end with predation rates averaging 10% per annum and up to 45% during episodic periods of intense predation (Isbell 1990).

If fire reduces the threat of predation, or decreases risk in dangerous places I expect that this too will shape range use. Using behavioral data documenting vigilant behaviors I found that vigilance strategies differed across habitats, but more importantly, all types of vigilance were significantly lower in burned areas regardless of habitat type (see Figure 3.1). For ecologically tethered species such as vervets, access to, and high predation risk within, savanna habitats may prohibit extensive use outside of burning events. I hypothesize that burning facilitates access to savanna foods by removing dense ground-level vegetation thereby reducing risk and increasing search efficiency. Given these improvements, burning likely enabled primates to take advantage of grassland habitats otherwise too dangerous to occupy.

Finally, I examined the spatial behavior of vervets postfire (Chapter 1; Herzog et al. 2014). In response to the 2012 controlled burns that altered a significant portion of savanna habitat directly adjacent to vervets' home range, subjects quickly expanded into the newly burned area (Herzog et al. 2014). Postfire, their home range increased in size by 91% (see Figure 1.2). This expansion was primarily located in newly burned areas, rather than general diffusion at territorial boundaries; with burned area representing 75% of the newly acquired territory. Postburn the study troop spent a much larger portion of their time outside of closed-canopy riverine habitats (preburn 16% of all [foraging] time was spent in grass subhabitat compared to 24% postburn). These data suggest that positive alterations in burned habitats created an impetus for a move away from closed canopy habitats and into the savanna. I hypothesize that the decrease in ground-level vegetation postburn facilitated travel, decreased the costs associated with searching for and acquiring prey, and lowered risk in general, the combination of which served as a strong motivator in the range expansion observed.

4.4 Discussion

"[T]here might have been a more than fortuitous association between natural fires and hominid activities… In time, these activities might have led to hominids' aiding and

abetting natural outbreaks of fire" (Dennell (1989: pg. 12). In the final portion of this paper, I use the quantifiable aspects of behavior associated with passive fire use among nonhuman primates to help identify the series of steps that led to fire dependence in our own lineage. The patterns of burn-area exploitation by savanna-dwelling monkeys reported here draw our attention to several behavioral traits associated with passive fire use. Drawing on these data, I generate hypotheses regarding the ways in which a shift from passive to active fire use could have shaped Plio-Pleistocene hominin evolution.

4.4.1 Fire and foraging improvements

Across many settings, nonhuman primates have been observed foraging in burned landscapes; consuming cooked foods within, and taking advantage of increased densities of invertebrate prey (for a review see: Herzog et al. 2014). These behaviors indicate that savanna-dwelling primates understand the implications of fire, they also suggest a deep phylogenetic foundation for passive fire use (Pruetz and LaDuke 2010). Within burned landscapes, nonhuman primates benefit from increased encounters with high-ranked prey items. Here, I focus on foraging improvements for mobile invertebrate prey, and underground storage organs (USOs, geophytes, or loosely, tubers) because both sets of resources have been nominated as central to early hominid diets (for reviews see: O'Connell et al. 1999; Bogart and Pruetz 2011; McGrew 2014; Sayers and Lovejoy 2014).

We now have a substantial amount of data confirming that our genus emerged at a time of increasing aridity and climatic variability. These ecological changes may have limited the availability of previously profitable foods (Reed 1997; Hawkes et al. 1998; Potts 1998; Cerling et al. 2011). Under these circumstances, both the addition of novel or difficult to acquire foods and the uptake of new technology to process lower ranked foods is necessary (Hawkes and O'Connell 1992; Hawkes et al. 1997; O'Connell et al. 1999; Liebl and Martin 2014). In response, some hominin lineages broadened their diets, moved away from frugivory and focused instead on plant and animal foods abundant in grassland settings. Strontium analyses highlight this shift, identifying an uptake in insects, tubers,

or a combination of the two in gracile *Australopithecus* diets (Sponheimer et al. 2005).

Entomophagy, or invertebrate consumption, remains a common feature of many human and nonhuman primate diets (DeFoliart 1999; McGrew 2001; Raubenheimer and Rothman 2013; Raubenheimer et al. 2014). The energetic payoffs for invertebrate consumption are relatively high (though often variable) even for larger-bodied primates (McGrew 2001; Bogart and Pruetz 2011; O'Malley and Power 2012; Isbell et al. 2013; O'Malley and Power 2014; Herzog et al. 2015). Much has also been made of the macronutrient contributions of insects to the diets of both human and nonhuman primates, with special focus on the high energy, fat and protein content of these prey (Raubenheimer and Rothman 2013; Raubenheimer et al. 2014; Rothman et al. 2014).

Given these positive attributes, one may ask, "why are bugs not a staple food for all larger bodied primates?" Often, the relatively small contribution of invertebrates to the diets of large bodied primates is attributed to the relative costs of pursuing small, mobile, difficult to acquire prey. Larger bodied primates must encounter invertebrates in larger quantities to balance the energetic costs of pursuit. As shown here, and elsewhere (Jaffe and Isbell 2009; Herzog et al. 2015), fire may act as an invertebrate magnet, drawing insects into burned areas and aggregating them in spatially bound patches. However, these changes are not consistent through time. Fire may act on the distribution of insects in three temporally distinct phases: (1) immediately post fire cooked carcasses may be easily retrievable and/or mobile prey fleeing from fire may be stunned or immobilized by the smoke and flames making their capture easier, (2) within the first weeks of burning invertebrates may become isolated in unburned refugia within the broader landscape of the burn and so aggregated may be easy targets for foragers, (3) following primary regrowth (4-20 weeks depending on burn season and habitat) invertebrates may repopulate burned areas in large numbers to feed on nitrogen-rich new shoots (Swengel 2001).

While fire-driven alterations in invertebrate distribution are clearly beneficial for large bodied primate foragers, positive changes are temporally limited. Fire also plays an

important role shaping the phytogeography of pyrophillic plants often creating long-term positive alterations in their distribution. Improvements in encounters with these perennial plant foods often come at a later date. For example, larger numbers of tuber-bearing plants are often observed the season following a fire, a pattern which may persist for several years (Le Maitre and Brown 1992; Gott 2005; Lamont and Downes 2011; Clarke et al. 2013). Other economically important surface plants such as melons and legumes are similarly stimulated by fire (Wiessner pers. comm.; Hargreaves 1996). In addition, many tuber producing plants are positively stimulated by increased harvesting (Thoms 1989; Anderson 1997; Anderson et al. 2012). If fire both stimulates recruitment of new plants, and encourages harvest by hominin foragers, this compound effect could largely alter the distribution and availability of tuber foods, an incentive that would only serve to promote continual landscape burning.

Fire's impact on tuber distribution is important not only because greater availability can improve overall forager returns, but also because tuber profitabilities can be improved markedly by cooking. Perhaps this is why, across many ecological settings, tubers serve as a primary food source for contemporary hunter-gatherers. The extensive use of wild tubers by traditional populations, is perhaps best documented among the Hadza of eastern Africa. Ethnographic work with this group has highlighted their reliance on tubers year round (Vincent 1985; Hawkes et al. 1989; Hawkes et al. 1997; Marlowe and Berbesque 2009). During difficult times, tubers provide one of the only means of meeting minimum energetic requirements. Yet, unlike berries, small children are not able to handle them effectively (Hawkes et al. 1995). Weaned Hadza children depend on their mothers to handle difficult to acquire foods to meet their energetic requirements. However, when a new sibling is born, it is their grandmothers who subsidize them (Hawkes et al. 1997). By this pathway, it is grandmother's effects that could account for the increased longevity, late maturity, and shorter birth intervals that distinguish us from the other living hominids (Hawkes et al. 1998; Kim et al. 2012, 2014; see Hawkes and Coxworth 2013 for a review). A shift to environments where weanlings are no longer able

to meet their own energetic needs is central to the grandmother hypothesis. If savanna habitats lacked infant-friendly foods, the systematic use of naturally burned landscapes likely served as a foundational technological advance because the distribution of tubers and insects, important food sources for savanna-dwelling hominins, are significantly positively altered by natural fires.

Early savanna-dwelling hominins may have relied heavily on these fire-mediated ecological changes. If so, the pronounced increases in body size apparent in *Homo erectus* may have arisen simply from a pattern of sophisticated passive fire use. First, grandmothers taking advantage of foods made abundant and edible by fire were able to subsidize food energy and expand the energy budgets of their daughters and dependents. The efforts of especially vigorous oldsters altered adult mortality in two important ways: 1) the junior kin of vigorous older females would carry fewer deleterious alleles expressed near menopause; 2) young adults with helpers would be able to achieve higher reproductive success, allowing a shift in the tradeoff between allocation to current reproductive effort and maintenance for later vigor. In both scenarios, selection against senescence decreased adult mortality and ultimately resulted in increased body mass (O'Connell et al. 1999; Pontzer 2012a). Further, a combination of improved diet, allomaternal subsidies, reduced travel costs, and the later addition of cooked foods may have enabled the encephalization of *H. erectus* (Navarrete et al. 2011; Fonseca-Azevedo and Herculano-Houzel 2012).

4.4.2 Fire and predator/prey relationships

The predator guild of lower Pleistocene eastern African was impressive. At least ten genera of large mammalian predators (Treves and Palmqvist 2007; Hart and Sussman 2009), and one species of predatory eagle (Hart and Sussman 2009) existed coeval with hominins (both *Australopiths* and *Homo*) Archaeological and isotopic evidence indicate that, at minimum, hominins were common prey of African eagles (Berger and Clarke 1995; Berger and McGraw 2007; Gilbert et al. 2009), and several species of large cats (Brain 1983;

Lee-Thorp et al. 2000). As hominins moved into increasingly arid, grass-dominated settings, their risk would have been elevated. Savanna settings lack tall trees and canopy cover, and the majority of biomass is located close to the ground in the form of herbaceous grasses, small shrubs and bushes, and low-growing trees. This thick ground cover inhibits visibility, making it difficult to detect both predators and potentially lethal threats. The lack of canopy cover also makes retreats to arboreal refuges impossible, leaving animals to engage in predator avoidance behaviors that increase the horizontal distance between themselves and pursuers. Given this set of constraints, many have argued that aspects of hominin morphology and behavior have been shaped by this threat (Treves and Palmqvist 2007; Hart and Sussman 2009; Hart and Sussman 2011). Some have suggested that fire control itself originated as a form of predator defense (Clark and Harris 1985; Brain 1995; Burton 2009). Data presented here support ecological motives for the origin of fire-use but once control was achieved, fire may have played a role in keeping nighttime predators away, just as it does today among contemporary peoples (Wrangham and Carmody 2010).

Although we do not know when hominins first used fire to protect themselves, we do know that fire negatively impacts the short-term distributions of many predators. When lion and serpent responses to burning are quantified, their densities in recently burned habitats are decreased (Wilgers and Horne 2007; Eby et al. 2013). Other mammalian predators (leopards and civets) are absent entirely (Ogen-Odoi and Dilworth 1984). For ambush predators, fire's removal of ground cover makes hunting attempts almost entirely impossible. Snakes on the other hand, are much more susceptible to avian predators in the exposed expanses of burned landscapes. The dearth of predators and threats in burned habitats is reflected in the behavior of primates foraging in burned areas. Within the burn, vervets elicit fewer vigilant calls and display fewer vigilant behaviors (Chapter 3; Jaffe and Isbell 2009). If the basic behavioral repertoire of stealth/ambush predators has remained constant through time (for a review see: Treves and Palmqvist 2007), we can expect similar behavior in burned habitats in the past. As

demonstrated here, burned savannas provide relatively safe refuges from predators and offer improved postencounter energetic returns. Given these positive alterations, the incentive to move into burned areas could have been substantial.

4.4.3 Range expansion and hominin dispersals

While exploiting burned areas nonhuman primates move more quickly and cover greater distances than in unburned areas (Chapter 1; Jaffe and Isbell 2009; Herzog et al. 2014). In as short a time-span as 4 months vervet subjects at Loskop Nature Reserve in South Africa doubled their home range, expanding primarily into burned landscapes. Data presented here (Chapter 2 and Chapter 3) suggests that increased foraging efficiency (i.e., improved encounter rates and higher profitabilities) and improvements in threat detection enable terrestrial foragers to meet energetic requirements in burned landscapes, moving a population previously tethered to forested habitats onto the savanna. Of course, the comparison between temporally-limited primate home range expansions and long-term hominin dispersals is limited. Vervets, unable to manipulate fire, are constrained to expansion into areas already burned. Once vegetation returns, home ranges appear to retract to their preburn state. This scalar issue aside, the degree and rate of vervet expansion may provide relevant data for modeling the earliest advances of hominins into fire-prone savanna settings.

Early hominin taxa retained primitive traits facilitating arboreal movement (Pontzer 2012a) suggesting continued dependence on closed canopy habitats; however, *Homo erectus* appears to have moved away from this retention. *H. erectus* is a larger bodied primate with fewer postcranial adaptations suited to climbing (Pontzer 2012a). Larger bodied animals have larger ranges (Swihart et al. 1988), and we see evidence of expansive dispersals soon after the emergence of *H. erectus*. If these anatomical and physiological adaptations reflect the end product of selective pressures related to the exploitation of burned landscapes, they suggest an early introduction to fire use. Once a pattern of fire exploitation is established, a scenario where early humans follow the

margins of successive burns, or create their own landscape fires into new frontiers, may have led to expansion at an astounding rate. Such a pattern of population movement along profitable patches has been hypothesized as the mechanism by which *Homo sapiens* quickly migrated through southern and Southeast Asia and on to Australia (O'Connell and Allen 2012). If fire creates profitable patches, its use as a landscape modification tool could have supported a similar pattern of *H. Erectus* dispersals out of Africa at ~1.8 MYA (Gabunia et al. 2001, Antón and Swisher 2004; Mellars 2006; O'Connell and Allen 2015).

4.4.4 Final remarks

While nonhuman primate foragers may be able to take advantage of burned areas where they exist, they cannot control fire or use fire to manipulate their own landscape. A hallmark of humans is dependence across the globe on controlled combustion (in the many forms that technology takes). By examining the dietary choices of savanna-dwelling primates in the presence of fires we can identify fundamental opportunities within burned patches. When hominins were able to more effectively exploit improvements in encounters with high-ranked prey created by burning, they moved beyond passive fire use and ultimately gained the tools for active manipulation. Improvements in search efficiency and achieved profitabilities, in combination with decreased predation risk may have acted as a catalysts for future fire control in a population of primates committed to savanna settings. The role of fire in shaping many of our genus' most distinctive traits has often been overlooked, the data presented here highlight the potential role of both passive and active fire use in each of the three traits outlined above:

- *shifts in diet*, a reduction in search costs appears to be one of the primary foraging benefits of fire-modified landscapes. This opportunity can be realized by active and passive pyrophiles alike. While nonhuman primates are limited by the intermittent and unpredictable nature of wild or anthropogenic fires, continued exploitation of these opportunities may serve as the foundation of obligate fire use. If hominins were able to similarly capitalize on burning events, they would

have had greater access to, and achieved better returns from, two key savanna resources: tubers and invertebrates. Aiding and abetting natural outbreaks of fire could have prolonged positive outcomes:

· *expansion of geographical range*, within burned landscapes foragers are able to move more quickly, and because of the positive changes in prey encounters and profitabilities are able to meet their energetic needs in habitats otherwise too dangerous or impoverished to use. Given these improvements, foragers should be able to colonize burned habitats, expanding well beyond previous ranges constrained by diet and habitat structure. If continuous, or contiguous, burning can be achieved, hominins may have been able to permanently move into previously uninhabited landscapes, and if necessary create profitable patches and extend attractive habitats.

· *increased body size and elongated life histories*, may have been driven by two fire-related phenomena. First, a reliance on more abundant, and potentially cooked foods, could have enabled the benefits of grandmothering to take off; the effects of which include longer adult life spans, delayed maturity, and larger adult body sizes. Second, fire may have reduced adult mortality by decreasing predation and lethal encounters with other dangerous animals in savanna settings which could also have driven longer adult lifespans, and ultimately larger adult body sizes.

The vervet data show that passive fire exploitation is a shared trait within the primate clade. As such, we can, and should, expect that our earliest ancestors used fire in a way similar to that described for vervets and other savanna-dwelling primates (Pruetz and LaDuke 2010; Herzog et al. 2014). Following this trajectory, controlled fire is the last step in a series of increasingly technologically demanding uses of fire, the evolutionary impacts of which should occur at an early date in hominin evolution. If the path to fire-dependence began with advantages of exploiting burns, the real “origins of fire use” will not be archaeologically visible. Rather, the archaeological evidence of fire use may indicated shifts in resource choice, population densities, technological advancement, and

site distribution (Parker 2014). To understand how our species moved from passive to active fire-use requires an exploration of the ways in which other members of our genus interact with fire. Investigating nonhuman primate responses to fire-mediated ecological change from the theoretical perspective of behavioral ecology can enable researchers to generate testable hypotheses and to propose alternative lines of evidence. Here, I have approached the problem of the origins of fire use from that perspective, the patterns outlined offer one place (of many) to begin to build an evolutionary model of fire-dependence.

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